SYMBOLAE BOTANICAE UPSALIENSES XI: 6
ARBETEN FRÅN BOTANISKA INSTITUTIONERNA I UPPSALA
UTGIVNA AV PROF. E. MELIN OCH PROF. J. A. NANNFELDT

STUDIES ON THE GROWTH AND THE OSMOTIC CONDITIONS OF ROOT HAIRS

BY

IVAR EKDAHL

UPPSALA 1953
A.-B. LUNDEQUISTSKA BOKHANDELN
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SYMBOLAE BOTANICAE UPSALIENSES

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STUDIES ON THE GROWTH AND THE OSMOTIC CONDITIONS OF ROOT HAIRS

INAUGURAL DISSERTATION

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OF UPPSALA WILL BE PUBLICLY DEFENDED IN THE BOTANICAL AUDITORY,
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IVAR EKDAHL
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Preface.

Root hairs are emergences from root epidermal cells. The formation of root hairs increases the surface of plant roots and consequently the contact between the roots and the surrounding medium (SACHS 1865, 1874). The enlargement of the root surface by development of root hairs is found to vary with the external conditions (PERSEKE 1877 pp. 23–25; SCHWARZ 1883 pp. 139–141; SNOW 1905 p. 14; WILSON 1936 p. 136; DITTMER 1937 p. 419, 1949; EVANS 1937, 1938; LUNDEGÅRDH 1946 p. 5). In some cases the enlargement of root surface by the formation of root hairs can be rather great and SNOW found that the surface of root hairs was about 30 times the surface of the mere roots of radish plants and about 40 times the surface of white mustard roots. The roots of higher land plants perform the absorption of inorganic salts and water, and SACHS already demonstrated the importance of root hairs for these vital processes. During the last century root hairs were repeatedly the subject of physiological investigations but although several important results have been reached, there are still many problems to be solved before we can attain definite knowledge of the physiology and the detailed function of root hairs. The present paper intends to give some new views on the growth of root hairs.

The present investigation has been carried out at the Institute of Plant Physiology of the Royal Agricultural College of Sweden, Uppsala. I wish to express my sincere gratitude to Professor HENRIK LUNDEGÅRDH, my chief and the Director of the Institute, who has introduced me not only into the studies of the root hairs but also into the different research problems of the Institute. I am deeply grateful to him for the valuable support and the great interest he has always given me and my investigations and for his kind permission to let me use the laboratory outfit of the Institute and for placing assistants at my disposal.

I am deeply indebted to Professor ELIAS MELIN, Director of the Institute of Physiological Botany of the University of Uppsala, for the great courtesy and kindness he has shown me from my first days as a botanist at Uppsala. I also wish to thank him for including this thesis in "Symbolae Botanicae Upsalienses".

To my teacher in Plant Physiology, Professor M. G. Stålfelt, Director of the Institute of Plant Physiology of the University of Stockholm, I convey my warmest thanks for valuable instruction, good advice and for his lively interest in my work during my time at the University of Stockholm and later.

For his kindness to me and for his interesting lectures I shall always keep in grateful memory my other teacher in Botany in Stockholm, the late Professor Otto Rosenberg.

I am much indebted to Professor Hans Burström, Director of the Botanical Laboratory of the University, Lund, for valuable discussions and advice during his time at the Institute of Plant Physiology of the Royal Agricultural College.

I also wish to give my warmest thanks to my colleagues at the Institute, Laborator Börje Åberg and Mr. Göran Stenlid, Fil. lic., for many interesting discussions, valuable advice and criticism.

Professor Folke Skoog, University of Wisconsin, Madison, U.S.A., has had the great kindness to revise the English text in spite of his busy engagement in other work. I want to express my deepest gratitude to him for the great care he has devoted to my paper.

To Miss Astrid Guilletmot, Fil. kand., of the Library of the Royal Agricultural College, I convey my best thanks for her readiness to facilitate my work and for her valuable help in the proof-reading.

I am deeply indebted to my wife, Mrs. Kerstin Ekdahl, for her unflinching support and I want to express my great appreciation of her valuable and assiduous help with the completion of the manuscript.

Finally, I wish to express my thanks to the laboratory members of the Staff of the Institute for careful help with the cultivation of the plant material and their assistance in the experiments.

Uppsala, Institute of Plant Physiology of the Royal Agricultural College, May 1953.

Ivar Ekdahl.

1. Introduction.

In 1944 professor H. LUNDEGÅRDH suggested to me to make a study of the difference in permeability between young, growing and old, mature root hairs. After rather much work it seemed evident that it was almost impossible to solve the problem with intact, living root hairs as a material. The studies were especially difficult because of the very active protoplasmic streaming in the hair-forming as well as in the surrounding cells, the streaming causing a transport of ions and cytoplasmic material, which could not be determined. Besides this investigation some broader studies of the physiology of root hairs were carried out at the Institute and some results from these investigations have already been presented (LUNDEGÅRDH 1946; KOPP 1948; EKDAHL 1948).

My studies presented in this paper are made as a completion of LUNDEGÅRDH's observations as to the osmotic conditions of root hairs and the fact that root hairs are not influenced by indole-3-acetic acid solutions in concentrations, which inhibit the growth of the roots (LUNDEGÅRDH 1946 p. 17, fig. 17), the last phenomenon having already been indicated by MEESTERS (1936).

In the case of roots grown in moist sawdust, where they are not quite turgescent, URSPRUNG and BLUM (1921) have shown that the "suction force" of the cells ("suction tension", "water-absorbing power", "diffusion pressure deficit", see URSPRUNG and BLUM 1916; URSPRUNG 1935; MILLER 1938 p. 93; MEYER 1945; MEYER and ANDERSON 1946 p. 148) increases stepwise from the epidermis inwards through the parenchymal cells and reaches a maximum value in the cells bordering on the endodermis. In contrast, a root grown in distilled water gave "suction force" values of zero in all cells of the epidermis as well as the parenchyma layers (URSPRUNG and BLUM 1921 p. 73, table 2). BURSTRÖM (1942 a p. 5) has shown that the epidermal cells of young wheat seedlings grown in dilute nutrient solution were fully turgid and that the "suction force" of the cells was zero, *i.e.* the turgor pressure of the cells was the same as their osmotic pressure. In studies of the same material the author has confirmed BURSTRÖM's results. 1–2-week-old wheat plants grown in weak nutrient solution had fully turgescent roots and root hairs even under conditions of high rates of transpira-

tion in the leaves. Measurements of the elongation rate of intact root epidermal cells have shown that this fact holds true also for immature, growing cells. In his work LUNDEGÅRDH (1946) has shown that the root hairs have a high turgor pressure and that their elongation rate is not immediately influenced by increases of the osmotic pressure of the external medium. Furthermore, LUNDEGÅRDH has pointed out the important difference between root hairs and roots in sensibility to high concentrations of indole-3-acetic acid solutions.

The root hairs elongate by a strictly apical growth (LUNDEGÅRDH 1946, 1950; HABERLANDT 1887 a, b; REINHARDT 1892, 1899; and others), a special type of cell elongation, in which the stretching is located in the apical portion of the hair. The hairs are usually produced in the region of the root, where cell elongation is still in progress, and they continue to elongate for several hours after the growth of the wall in all other parts of the cell has stopped (*cf.* JEFFS 1922, 1925 p. 584; SINNOTT 1939; SINNOTT and BLOCH 1939 a; BURSTRÖM 1941; BRUMFIELD 1942; CORMACK 1945; EKDAHL 1948). Whereas growth of the root hair is confined to the extreme tip portion of the wall, the growth of the epidermal cells proper — which form the hairs — occurs in all portions of the wall although at unequal rates in different zones of the cell surface.

Thus, there seem to be many facts which indicate that root epidermal cells with hairs are very suitable objects for studies of differential growth of the cell wall, especially as the growth of the hair and of the parent cell itself seems to be caused by two apparently different mechanisms.

During the last few years the author has carried out an extensive investigation of the growth of root hairs with special reference to the osmotic conditions of the hair-forming cells, and the consequences of changes in the turgor pressure of the cells on the growth and function of the hairs.

In an earlier publication (EKDAHL 1948) data have been presented on the growth of root hairs in normal nutrient solution and the action of chlorate and some related substances on the hairs. The present paper deals with some observations on the extensibility of the cell wall of growing root hairs, the osmotic pressure of the hairs, and the resistance of their cell walls to changes in the turgor pressure. The problems studied and discussed have in many cases connections with my earlier experiences. Further evidence will be presented in the future with regard to the effects of some growth substances on the growth of root hairs and roots, the relation between the elongation rate of the hairs and the position of the nucleus in the hair, and the consequences of the increase of the root surface through the development of root hairs for the absorption of nutritive ions.

The root-hair-forming cell can be subdivided into two parts, the longi-

tudinal ("epidermal") part, which is in direct contact with the neighbouring epidermal and cortical cells, and the hair, which protrudes laterally to the root surface. To distinguish between these two parts the former will be referred to as the *hair-cell* and the latter as the *hair*.

2. Material and methods.

The observations and the measurements have been made on epidermal cells and root hairs of *roots of intact seedlings* of spring wheat (variety Diamant II) grown in nutrient solution under artificial illumination in a temperature control cabinet constructed and described by LUNDEGÅRDH (1932 pp. 10–20). The cultivation conditions have been those continuously used at this Institute, and previously described by LUNDEGÅRDH (1943), EKDAHL (1944, 1948), and ÅBERG (1946, 1948). In most experiments 3–4-day-old seedlings have been used. The elongation rate and some of the reactions of the root hairs have been studied on roots growing in an observation chamber with flowing nutrient solution, placed on the stage of a microscope and with arrangements for changing the medium without interrupting the flow of nutrient solution. The observation chamber was a modification of that constructed and described by LUNDEGÅRDH (1946). A special apparatus was made to obtain continuous aeration of the stock solutions and the solutions in the containers, from which the media flow into the observation chamber. The entire apparatus was placed in a temperature control cabinet kept at 20–21° C. Most of the measurements and observations were carried out in this cabinet. The main features of the experimental procedures have been described in detail in a previous paper (EKDAHL 1948 pp. 115–118). Special arrangements will be mentioned in connection with the descriptions of the individual experiments. The ordinary nutrient solution used, the standard solution (*S*-solution), has the following composition:

	Concentration in millimoles per litre
KNO_3	0.6
$Ca(NO_3)_2$	1.5
$MgSO_4$	1.0
KH_2PO_4	1.2
Na_2HPO_4	0.4
Fe-NH_4-citrate	0.03
B, Cu, Mn, Zn	traces

The pH of the solution varies between 6.0 and 6.3. All test-solutions were prepared from double-distilled water. The osmotic pressure of the *S*-solu-

tion is calculated to be about 0.3 atm. (= S atm.). Boron, copper, iron, manganese and zinc (mixed together in one of the stock solutions) were omitted in the solutions used in the observation chamber in order to avoid precipitation of iron compounds (see EKDAHL 1948 p. 114).

3. The concepts of osmotic quantities.

The terms *osmotic pressure* and *turgor pressure* are used in accordance with the definitions given by MEYER (MEYER 1938, 1945; MEYER and ANDERSON 1946; see also CRAFTS *et al.* 1949), and the quantities are expressed in atmospheres at 20° C. In addition, the term *osmotic value* will be used to denote the numerical value of the osmotic pressure in atm. at 20° C.

Osmotic pressure is used to designate "the maximum pressure which develops within a solution under certain ideal conditions" (MEYER 1945 p. 151; see also MEYER 1938 p. 532; MEYER and ANDERSON 1946 p. 94). In a wider sense "it is a common practice to speak of solutions as possessing an osmotic pressure whether they are under such conditions that a pressure can develop within them or not" (MEYER and ANDERSON 1946 p. 95).

Turgor pressure is used to designate "the *actual* pressure developed as a result of osmosis" (MEYER 1938 p. 533; see also MEYER 1945 p. 154; MEYER and ANDERSON 1946 p. 95).

To demonstrate the osmotic quantities of the cells studied the following symbols have been chosen:

O = osmotic pressure
O_c = osmotic pressure of the cell content
O_e = osmotic pressure of the external medium
T = turgor pressure of the cell content

The osmotic quantities of root epidermal cells and root hairs have been studied either at full turgor (water-saturated stage) *or at incipient plasmolysis* (def. see MEYER and ANDERSON 1946 p. 136). At the first stage the ability of the mature cells to increase in length by osmotic uptake of water is zero and the equilibrium condition is expressed by the equation: $T = O_c - O_e$. At the second stage (incipient plasmolysis) the cells have a great ability to absorb water. The turgor pressure is zero ($T = 0$) and the osmotic pressure of the cell (O_c at incipient plasmolysis, or O_{cip}) is equal to the osmotic pressure of the external solution.

The walls of plant cells are mostly not quite rigid, but they are extended by the turgor pressure. The term *turgor extension* is used to designate the

difference between the initial length of the turgid cell and the length after plasmolysis, the difference being given in microns or in per cent of the initial length. The values of turgor extension presented in this paper refer to measurements of hair-cells and root hairs at the completely turgid stage.

4. The turgor extension of mature hair-cells.

In studies of the osmotic conditions of root hairs it is of great importance to know the extensibility of the cell walls of the mature hair-cells from which the hairs emerge. In his investigations of the osmotic conditions and the elasticity of the walls of epidermal cells of wheat roots, BURSTRÖM (1942 a, b) found that the turgor extension (percentage elastic extension) of the walls of mature cells was very low. Investigations of the present material, including roots of wheat seedlings, but grown under conditions different from those used by BURSTRÖM, have given the same results. The determinations were carried out on *intact roots* of 3–4-day-old seedlings (exp. no. 65, table 1), the roots being grown in the observation chamber for some hours before the observations (see EKDAHL 1948 p. 114). The measurements of length of the turgescent cells were made on roots placed in dilute nutrient solution in which the root hairs grow much better than in distilled water. The osmotic pressure of the *S*-solution is so low that it can be neglected ($S = c.$ 0.3 atm.). The length of some epidermal cells was measured and the flowing nutrient solution was then quickly changed to a solution of sodium chloride with an osmotic pressure of 11.2 atm. This causes a conspicuous plasmolysis of the epidermal cells to take place and can be clearly seen within an hour. The length of the plasmolyzed cells was measured, and the decrease in length was calculated. On each root measurements were made on groups of cells placed at distances of 5, 10 and 20 mm from the root tip. The cells 5 mm from the tip were still elongating, and in this region the root hairs had a length of up to 50 microns. The cells at 10 and 20 mm distance from the tip, respectively, were mature but all the root hairs emerging from the measured cells were still elongating. The results, given in table 1, show that the turgor extension of the longitudinal walls of mature hair-cells is less than 2 per cent. If we consider a mean extension of 1.5 per cent, and assume that the extension of the transverse walls is the same per unit length as that of the longitudinal walls, the decrease in volume after plasmolysis will be about 4.5 per cent. It has not been possible to make accurate measurements of the changes in dimensions of the transverse walls of the epidermal cells of intact roots.

Table 1. The turgor extension of growing and mature hair-cells of wheat seedlings.

Experiment no. 65.
3–4-day-old seedlings. Plasmolysis conditions see the text p. 11.
Each value is the mean of the measurements of ten roots.

Distance from the root tip mm	Growing stage	Turgor extension %	Number of measured cells
5	growing	11.2	46
10	mature	1.5	30
20	mature	1.2	32

5. The turgor extension of growing root hairs.

Under the given conditions the root hairs of young wheat seedlings grow very well and form extremely narrow and long cylindrical emergences (*cf.* EKDAHL 1948). The different parts of each hair are very uniform in cross section except that the base is a little wider, and the growing apex tapers off gradually and has a thinner cell wall than the rest of the hair. The hairs may reach lengths of 1 to 2 mm, but have diameters of only 10 to 15 microns.

Attempts have been made to determine the turgor extension of the cell wall in both the longitudinal and the transverse directions of the hairs. The longitudinal extension was calculated from differences between measurements of the hair length in *S*-solution and after plasmolysis (exp. no. 66, table 2). The length of the root hairs has been determined with an accuracy of $\pm$ 0.2–0.5 per cent. The hairs are plasmolyzed in the following manner. The flowing *S*-solution is made weakly hypertonic by introducing NaCl or glucose (S + 9.0 atm.). After 10 to 15 minutes this solution is made still more hypertonic (S + 11.2 atm.). In this way the root hairs are slowly plasmolyzed and the protoplast is only loosened from the cell wall at the extreme apex at first (plate I: fig. 1 b). As plasmolysis proceeds, the protoplast contracts downward in the hair until an equilibrium state is reached (plate I: fig. 1 c). The equilibrium is always realized within one hour after the first change of solution, and then the second measurements of the length of the hairs are made. The results of the determinations, presented in table 2, show that the total decrease in microns is very small. In fact, for hairs longer than 100 microns the decrease is smaller than 1 per cent and it is thus impossible to obtain any accurate values. If the growth of the hairs continues after the first measurements the real decrease in

Table 2. Turgor extension of growing root hairs of wheat seedlings.

Experiment no. 66.
3–4-day-old seedlings. Plasmolysis conditions see the text p. 12.
Each value is the mean of the measurements of ten roots.

Length of root hairs in μ	Number of root hairs observed	Turgor extension of root hairs	
		in μ	in %
<100	24	0.9	3
100–200	15	< 1	< 1
200–300	13	< 0.5	< 0.5
300–500	12	< 0.5	< 0.5

length will be higher than the calculated values. The contraction in per cent of the original hair length decreases with increasing length of the hairs. The results are the same if the medium is changed once more to a still more hypertonic solution (S + 13.4 atm., see plate I: fig. 1 d) or if the second measurements are made at the time of incipient plasmolysis of the tips or are delayed until two hours after the start of the treatment. Comparative studies of root hairs from other plant species have given similar results (exp. no. 67, table 3).

It must therefore be concluded that the turgor extension of the cell wall of root hairs in the longitudinal direction is very small (*cf.* Lundegårdh 1946). It must be remembered, however, that it is only the apex of the hair that elongates, and that the extensibility of different parts of the wall may be unequal.

In the case of sporangiophores of *Phycomyces* — which, like root hairs, elongate by an apical growth mechanism — Castle (1937 a, b) and others have established unequal stretching rates in different zones by marking the wall at the tip with spores of *Lycopodium* (see Castle 1942). All the elongation of the 3–5 cm long sporangiophores is found by Castle to be

Table 3. Turgor extension of growing root hairs of Helianthus, Sinapis and Zea seedlings.

Experiment no. 67. Plasmolysis conditions see the text p. 12.

Material	Number of root hairs observed	Turgor extension of root hairs	
		in μ	in %
Helianthus annuus	8	< 1	< 0.5
Sinapis alba	5	< 1	< 0.5
Zea mays	5	< 1	< 0.5

confined to the 1–2 mm long apical region, and they elongated at the rate of about 3 mm per hour (Castle 1940). Bünning (1937) found unequal elasticities in different zones of the elongating part of the sporangiophores of *Pilobolus* when the turgescence was lowered. The size of root hairs is much smaller than that of the sporangiophores mentioned, and it is therefore a more complicated problem to distinguish zones of different elongation rates in the hair by a marking method. Haberlandt (1887 a pp. 54–57), however, blew dry starch grains onto root hairs growing in a moist air chamber. In a few cases he succeeded in marking the hair apex without interrupting the growth. From these cases he determined that it was the very apex only, about 13 μ in length, that took part in the stretching. Reinhardt (1892 pp. 555–556, plate XXVI figs. 40–42), on the other hand, could not avoid stopping the growth of the hairs when he dipped roots into water with small particles of red-lead. After a time of growth stoppage, however, some of the marked hairs began to stretch again, and on these hairs Reinhardt could observe an unequal stretching of different parts of the tip calotte. In these cases, however, the unequal stretching zones of the apex were not placed in such a regular succession, calculated from the apical point of the hair, as Reinhardt had assumed for a root hair elongating with the ordinary uniformity (Reinhardt 1892 p. 556, compare also figs. 1–3 with figs. 41 A–41 C). Reinhardt did not consider the unequalities found between different parts of the hair tip wall as representative of the normal growth of the hairs.

The author has used nutrient solutions with suspended particles of India ink streaming through the observation chamber for marking root hairs but has failed to distinguish zones of different stretching rates in the apices of growing hairs (exp. no. 68). This must be due to the fact that the elongating part of the hair apex is very short. The measurements show that the part that elongates may actually be no longer than the diameter of the hairs, *i.e.* 10 to 15 microns. The length of the growing zone is found to be independent of the length of the hair.

If the differences in length between the hairs in the fully turgid and the plasmolyzed states are referred to the stretching zone only, the elasticity of this part of the cell wall will be 5 to 10 per cent for hairs shorter than 100 microns, or of the same magnitude as for the root epidermal cells during their elongation period (*cf.* table 1, and Burström 1942 a).

The turgor extension in the tangential direction of the cell wall of the hairs was determined by the same plasmolysis method as described before. The measurements, however, were made at other time intervals (exp. no. 69, table 4). The diameter of the root hairs has been determined with an accuracy of ± 1–2 per cent. The diameter of the mature part of the hairs was first determined in *S*-solution and following the change of medium the

Table 4. Decrease in diameter of growing root hairs of wheat seedlings after plasmolysis.

Experiment no. 69.

3–4-day-old seedlings. Plasmolysis conditions see the text p. 12.

Each value is the mean of the measurements of twenty hairs on each of three roots ($n = 60$).

Measurements	Root hair diameters in microns			Decrease in diameter, per cent of the diameter in nutrient solution	
	in *S*-solution	at incipient tip plasmolysis	after plasmolysis in hypertonic solution	at incipient tip plasmolysis	after plasmolysis in hypertonic solution
A	12.8	12.2	11.0	4.8	14
B	12.6	12.0	10.7	4.5	15
C	12.6	12.1	10.8	4.2	14
D	12.4	12.0	10.4	3.4	16
Mean	12.6	12.1	10.7	4.2	15

second measurements were made at the stage of the earliest visible plasmolysis or at the time of incipient plasmolysis of the tips (0 to 10 minutes after the change of solution). Later on the diameter of the hairs was measured one hour after the first change of medium, when the osmotic equilibrium with the plasmolyzing solution ($S + 11.2$ atm.) had been reached. The measured root hairs were 300 to 500 microns long, and the transverse contraction of the hairs was always uniform along the whole length of the hairs. The results are given in table 4.

At incipient tip plasmolysis the turgor pressure was zero, and the diameter of the hairs had decreased by about 4 per cent, but after one hour's plasmolysis the diameter had decreased by about 15 per cent. Thus, it is evident that the plasmolytic medium (NaCl-solution) influences the transverse contraction of the mature portion of the hair wall, and that the turgor pressure of the hairs seems to extend the mature wall quite differently in the transverse and in the longitudinal directions. This difference is visible not only after plasmolysis but also after plasmoptysis of the hairs. The term *plasmoptysis* was first used by FISCHER (1900, 1903, 1906) to designate the bursting of bacteria under unfavourable osmotic or other conditions. After plasmoptysis the turgor pressure of the root hairs must be zero and it has been found that the length of the hairs had decreased very little. If any decrease in length of the hairs was observed at all it was principally caused by the wrinkling of the wall, especially at the base of the hairs (see plate II: fig. 10 and EKDAHL 1948, plate XI: fig. B). After plasmoptysis, however, the diameter of the hairs decreased to the same extent

Table 5. Decrease in diameter of growing root hairs of wheat seedlings after plasmoptysis in nutrient solution saturated with nitrogen.

Experiment no. 70.

3–4-day-old seedlings. Plasmoptysis conditions see the text p. 12.

Each value is the mean of the measurements of twenty hairs on each of three roots ($n = 60$).

Measurements	Root hair diameters in microns			Decrease in diameter, per cent of the diameter in aerated nutrient solution	
	in aired *S*-solution	after plasmoptysis in nitrogen-saturated *S*-solution		after plasmoptysis in nitrogen-saturated *S*-solution	
		0–10 min.	60–70 min.	0–10 min.	60–70 min.
A	13.4	12.7	12.6	5.2	5.9
B	12.8	12.1	12.1	5.7	5.2
C	12.9	12.4	12.2	4.0	5.5
Mean	13.0	12.4	12.3	5.0	5.5

as after incipient plasmolysis. This will be apparent in more detail in the following experiments.

Plasmoptysis of root hairs can be caused by a number of changes in the external conditions (*cf.* Ekdahl 1948; Kopp 1948). Two ways of causing plasmoptysis are particularly suitable for measuring the turgor extension of the cell wall of the hairs. Kopp (1948) has shown that root hairs of wheat seedlings burst at their tips when they are transferred to nutrient solutions with no or low oxygen content (< 5 mg per litre). Further, Stiehr (1903) found that root hairs were plasmoptyzed when roots were immersed in sodium chloride solutions with concentrations lower than that isotonic to the cell content at incipient plasmolysis (*cf.* Ekdahl 1948; and p. 37).

Kopp used an experimental set-up similar to that used by the author. In a solution saturated with commercial nitrogen she found the oxygen content to be about 0.5 mg per litre (Kopp 1948 p. 286). This solution caused an anaerobic plasmoptysis of the root hairs within a few minutes after the change of medium.

The author has also made some observations on the effects of *S*-solutions poor in oxygen (exp. no. 70, table 5). Commercial nitrogen, purified by passing through alkaline pyrogallol solutions, was bubbled through the *S*-solution some hours before the observations and continuously during the whole experiment. Intact roots were placed in the ordinary observation chamber, but the chamber was sealed as tightly as possible with a mixture of paraffin and cocoa-butter in order to prevent air from passing into the

Table 6. Decrease in diameter of growing root hairs of wheat seedlings after plasmoptysis in 0.12 *M* NaCl-solution.

Experiment no. 71.

3–4-day-old seedlings. Plasmoptysis conditions see the text p. 12.

Each value is the mean of the measurements of twenty hairs on each of three roots ($n = 60$).

Measurements	Root hair diameters in microns			Decrease in diameter, per cent of the diameter in nutrient solution	
	in aired *S*-solution	after plasmoptysis in NaCl-solution		after plasmoptysis in NaCl-solution	
		0–10 min.	60–70 min.	0–10 min.	60–70 min.
A	13.0	12.3	11.2	5.1	13
B	13.2	12.6	12.0	4.2	9
C	12.9	12.3	11.4	4.8	12
Mean	13.0	12.4	11.5	4.7	11

streaming solution. The roots with their hairs were first allowed to grow in an air-saturated *S*-solution for some hours and then suddenly the flowing medium was substituted by the *S*-solution poor in oxygen (nitrogen-saturated). As in KOPP's experiments most of the growing hairs were plasmoptyzed within a few to ten minutes after the change of medium. In each observation series the diameter of the hairs was determined at three time intervals, in the *S*-solution just before the change of medium, 0–10 minutes after the change of medium (or just after the time of plasmoptysis), and 60–70 minutes later. The results are given in table 5, and they show that plasmoptysis causes a decrease of about 5 per cent in the diameter of the hairs and that this decrease is almost the same just after plasmoptysis as 60–70 minutes later.

In another series (exp. no. 71, table 6) the hairs were brought to bursting by a change of medium from *S*-solution to pure sodium chloride solutions (*cf.* STIEHR 1903; EKDAHL 1948). As will be shown later (pp. 39–40, tables 20 and 21), the highest percentage of plasmoptyzed root hairs was reached in solutions of 0.10 or 0.12 *M* sodium chloride. In the experiment in which a concentration of 0.12 *M* was used, the root hairs burst within a few to ten minutes after the change of medium. The diameter of the hairs was determined at three time intervals, in *S*-solution, 0–10 and 60–70 minutes after the change of medium, respectively (plate II: figs. 9–10).

In these two experiments (nos. 70 and 71) the plasmoptysis caused an immediate lowering of the hair diameter by about 5 per cent. Moreover,

Table 7. Changes in volume at incipient plasmolysis of mature hair-forming cells with growing hairs of different lengths.

Values calculated from the experiments nos. 65, 66 and 69. For the calculations see the text.

Length of root hairs μ	Decrease in volume at incipient plasmolysis %
300	5.3–5.9
500	5.8–6.5
750	6.0–7.1
1 000	6.4–7.4
1 500	6.7–8.0
2 000	7.1–8.3

the sodium salt solutions caused a further transverse contraction of the cell wall of the hair by 9 to 13 per cent in 0.12 *M* solutions and measured 60–70 minutes after the change of medium.

Thus, the three series of observations (exp. nos. 69–71) are in good agreement with each other. It is clearly shown that the turgor pressure causes the mature hair wall to extend only slightly in the longitudinal direction and by about 4 to 5 per cent in the transverse direction. The mature wall is further contracted in the transverse direction by the influences of sodium chloride solutions but is unchanged in the longitudinal direction.

With the help of the data given in tables 1, 2 and 4 the decrease in volume at incipient plasmolysis of a mature hair-cell and its growing hair can be calculated. The value obtained for the volume of the hair-cells is 1.1×10^5 μ^3 ($280 \times 20 \times 20$). The cell dimensions are based on measurements which will be dealt with in a later paper, showing that the hair-cells studied are mature at a mean length of 280 microns and that the cells have transverse walls which are, on an average, 20 microns in length in the tangential as well as in the radial direction of the root. The hair-cell itself decreases about 4.5 per cent in volume (*cf.* p. 11). The observed root hairs, more than 100 microns long, did not change appreciably in length after plasmolysis (table 2), but their diameters decreased by about 4 to 5 per cent at incipient plasmolysis (table 4). Thus, the hairs change in volume by about 8 to 10 per cent irrespective of their length. The decrease in volume at incipient plasmolysis of the whole hair-forming cells (hair-cell + hair) is dependent on the volume ratio between the hair and the hair-cell. The changes in volume obtained for cells with hairs of different length are presented in table 7.

6. The osmotic properties of growing root hairs.

The determination of osmotic properties of growing root hairs is complicated by the fact that the hairs are differentiated parts of the epidermal cells.

As mentioned, it is possible to plasmolyze the epidermal cells with their hairs in such a way that the protoplast is loosened from the cell wall only at the tip of the hair (p. 12), and in this way the state of incipient plasmolysis is easily determined.

Roots from 3–4-day-old wheat seedlings have been used for the determinations (exp. no. 72, table 8). The roots were placed in the observation chamber in flowing *S*-solution. At the start of the experiments the root hairs were observed to be elongating in an ordinary manner. The nutrient solution was then changed to a solution of sodium chloride, glucose, or sucrose, and the plasmolysis effects of the solutions were observed. In the first experiments the plasmolytic substances were added to the *S*-solution or the plasmolytic media consisted of solutions of sodium chloride, glucose, or sucrose, in which the osmotic value of the *S*-solution was compensated by addition of $CaCl_2$. Calcium chloride or the nutrient salts were added to the plasmolytic media in order to avoid swelling of the protoplasm (*cf.* HÖFLER 1939, 1940), but comparative observations have shown that there were no differences in the plasmolysis course caused by isotonic solutions with and without calcium chloride or the nutrient salts. Further, no differences could be found between the plasmolysis effects of isotonic sodium chloride, glucose, or sucrose solutions. Most of the determinations of the osmotic pressure of root hairs at incipient plasmolysis were carried out, however, by using solutions of pure sodium chloride in the concentration range from 0.14 to 0.24 *M* (0.14, 0.15, . . . 0.24 *M* NaCl). The osmotic values determined by WALTER (1936), have been used and were recalculated to be valid at 20° C, which was the temperature in the cabinet where the experiments were carried out.

One hour after the change of the flowing medium the percentage of the root hairs (300 to 500 μ in length) which showed incipient plasmolysis was determined. When between 50 and 100 per cent of the hairs showed signs of incipient plasmolysis, the root hairs were taken to be at the stage of incipient plasmolysis and their osmotic value was taken to be equal to that of the plasmolyzing solution used (*cf.* MEYER and ANDERSON 1946 p. 136). The minimum observable difference in osmotic pressure between different cells was 0.5 atm. (0.01 *M* NaCl). Each solution was tested on five to twelve roots, and for each observation 2 roots were placed side by side in the observation

Table 8. The osmotic pressure at incipient tip plasmolysis of growing root hairs of wheat seedlings grown in culture media with different osmotic pressures.

Experiments nos. 72 and 73.

3–4-day-old seedlings grown in *S*-solutions with the osmotic pressures increased by addition of different amounts of NaCl. Plasmolysis conditions see the text p. 19.

The decrease in cell volume at plasmolysis varies with the length of the root hairs (see table 7). Thus, the osmotic values of turgid root hairs are found to be 5 to 8 % lower than the observed values. Volume change is the difference between the volume of the hairs in full turgor and that at the incipient plasmolysis stage.

Osmotic pressure of the culture solution atm.	Osmotic pressure of root hairs at incipient plasmolysis atm.	Concentration of the plasmolyzing solutions *M* NaCl	Turgor pressure of completely turgid root hairs atm.	
			volume change 5 %	volume change 8 %
S	7.6– 8.5	0.17–0.19	7.0–7.8	6.8–7.6
0.5 + *S*	8.1– 9.0	0.18–0.20	6.9–7.8	6.7–7.5
1.0 + *S*	8.5– 9.4	0.19–0.21	6.8–7.7	6.6–7.4
2.5 + *S*	10.3–11.2	0.23–0.25	7.0–7.9	6.7–7.5
5.0 + *S*	11.6–12.5	0.26–0.28	5.8–6.6	5.4–6.3

chamber. The results are given in table 8 and show that root hairs grown in *S*-solution show incipient plasmolysis at the tip in solutions of 7.6 to 8.5 atm. osmotic values. Observations on the two roots from the same culture have always given the same result and, thus, the variations of the osmotic pressure in the table must refer to differences between material from different cultures. The osmotic pressure at the incipient plasmolysis stage of hairs of different length (200 to 1000 μ) has always been found to be equal, so that any differences that may exist must in all cases be rather small (<0.5 atm.). The very young hairs (<100 μ in length) have higher osmotic pressures at the incipient plasmolysis stage than the longer ones (*cf.* HILL 1908), but the hair-cells of the former are not mature and will therefore contract more than the hair-cells of the latter.

The method of incipient plasmolysis is found to be the only way to measure the osmotic pressure of growing root hairs. Of course, one must take into consideration that a small amount of the plasmolytic medium may be absorbed during the plasmolysis of the hairs, and that this general error of plasmolysis experiments is unavoidable in the present case because corrections for the rate at which the ions or the molecules of the plasmolytic media are absorbed by the contracting protoplast cannot be made in terms of measurements of the progress of deplasmolysis, as no deplasmolysis takes place even in hypotonic solutions. Deplasmolysis is impeded by the fact

that the free tip surface of the contracting protoplast very soon becomes covered by a new cell wall inside the original wall. This new wall will be left free inside the hair if the hair is plasmolyzed a second time with a more hypertonic solution (see plate I: fig. 2).

However, attention will be called to the fact that the same result is obtained whether the hairs are plasmolyzed by sodium chloride or by isotonic solutions of glucose or sucrose (*cf.* KOPP 1948 p. 295). This suggests that the absorption of the plasmolytic substances is too slow to increase the osmotic value of the hairs before the protoplasm is loosened from the wall at the tip, or that the permeability of the protoplasmic membrane of the root hairs is the same for sodium chloride as for glucose or sucrose. The former alternative seems more probable, and consequently the error caused by absorption of the plasmolytic substances would appear negligible.

Before the hairs show incipient plasmolysis a small amount of water may be lost from the cell, so that the volume of the hairs is decreased slightly. Thus, the osmotic strength of the cell sap at incipient plasmolysis (= the osmotic pressure of the plasmolytic medium) is a little higher than that of the sap of the intact, uncontracted hairs. The values of the osmotic pressure of the cells observed in the experiments refer to the incipient plasmolysis stage and are consequently a little too high as compared with the values of the cells in the intact, turgid stage.

Now we know the mean volume of the hair-cells with their hairs in the turgescent state and the decrease in volume followed by the plasmolysis (p. 18, table 7). Further, the osmotic pressure of the cells is inversely proportional to their volumes. Thus, as we know the osmotic pressure of the cells at incipient plasmolysis (O_{cip}), the volume of the fully turgid cells (V_{ct}) as well as the volume at incipient plasmolysis (V_{cip}), the following equation will give the osmotic pressure of the hair-forming cells at the fully turgid stage (O_{ct}):

$$O_{ct} = \frac{O_{cip} \times V_{cip}}{V_{ct}} .$$

It may be seen from table 7 that a hair-forming cell with a hair 500 microns long has decreased in volume at incipient plasmolysis by about 5.8 to 6.5 per cent, but a cell with a hair 2000 microns long has decreased about 7.1 to 8.3 per cent. Thus, the osmotic pressure of cells with longer hairs should be higher than that of cells with shorter hairs, if their osmotic pressures in the turgescent state are the same. The difference between them, however, is so small that it cannot be demonstrated directly by the plasmolysis experiments (see p. 20 and table 8).

Thus, the experiments show that the hair-forming cells of roots grown

in *S*-solutions have an osmotic pressure of 7.6 to 8.5 atm. at 20° C at incipient plasmolysis, and their osmotic pressure remains constant or varies only slightly during the whole period of elongation.

The effect of varying the concentration of the culture medium on the osmotic pressure of the root hairs was made the subject of special studies (exp. no. 73, table 8). The wheat seedlings were grown for 1 to 2 days in *S*-solutions in which the osmotic pressure was increased by addition of different amounts of sodium chloride. The incipient plasmolysis at the tip of the root hairs was then determined as described above (p. 19). The culture solutions used and the results of the observations are given in table 8. The results show that an increase of the osmotic pressure of the culture medium with up to 2.5 atm. is followed by an equivalent increase in the osmotic pressure of the root hairs. When the osmotic pressure of the medium was increased by 5 atm., however, the value of the hairs was increased by only 4 atm.

The volume of the mature hair-forming cells from *S*-solutions has been determined at incipient plasmolysis and at full turgor (see p. 18, table 7), and the osmotic pressure of the cell content at incipient plasmolysis has also been determined. The osmotic pressure of the cells is inversely proportional to the cell volume, and from the values obtained the osmotic pressure of the cell content in the fully turgid state, *i.e.* the normal state, can readily be calculated with the help of the formula given above.

The difference between the calculated value of the internal pressure of the cells in the fully turgid state (O_{ct}) and the osmotic pressure of the ordinary *S*-solution (O_e) will give the actual turgor pressure of the living, intact cells (table 8).

Measurements have shown that mature hair-forming cells of roots grown in *S*-solutions, with the osmotic pressure increased by addition of sodium chloride ($S + 2.5$ and $S + 5.0$ atm.), are fully turgid. If the transpiration rate was lowered the plants grown in these solutions started to guttate rather soon. It was also found that the turgor extension of these cells is similar to that of the hair-forming cells of roots grown in *S*-solution only (*S* atm.).

From the facts mentioned and the parallelism between the increase in the osmotic pressure of the medium and that of the internal pressure of hair-forming cells in the different culture media, it will be evident that the turgor pressure of the root hairs is the same for hairs from all the culture media with osmotic values between *S* and $S + 2.5$ atm., but in hairs kept in solutions with an osmotic pressure of $S + 5.0$ atm. the turgor pressure is lower (see table 8).

High osmotic values of root hairs have been found in several previous investigations, and the results of some of the more detailed ones may be

mentioned. STIEHR (1903) observed that root hairs of young *Phleum* seedlings were not plasmolyzed by a 1.3 % potassium chloride solution (7.7 atm.), but more or less by a 1.5 % KCl solution (9 atm.), and all hairs in a 1.9 % solution (11 atm.). Further, HILL (1908) found the osmotic equivalent of root hairs of two salt-marsh plants (*Salicornia* and *Suaeda*) to be 5.8 to 6.7 % sodium chloride. By transferring the plants into solutions with a higher osmotic pressure, HILL has shown that "the root-hairs can accomodate their internal osmotical pressure in proportion to the osmotical strength of the soil-water" (p. 139). For 16 different plant species grown in moist air ROBERTS (1916) has shown that the "osmotic pressure" of the root hairs was 5.1 to 7.7 atm., and for barley as high as c. 11 atm. ROBERTS, too, showed that the "osmotic pressure" of the root hairs of radish seedlings increased "almost in direct proportion" (p. 501) to the increase in concentration of the medium (0.0 to 0.65 *M* sucrose).

These data are in good agreement with the results presented above. The osmotic pressure of root hairs of wheat seedlings — as hairs of several other species — increases in direct proportion to the increase in osmotic pressure of the culture medium. Only in the most concentrated solutions is the rise in the osmotic value of the hairs somewhat less than the increase in the concentration of the medium.

7. The rigidity of the cell wall of growing root hairs.

In the previous chapter it was shown that the osmotic pressure of the root hairs is rather high. Thus, the tension of the thin, expanding membrane at the tip must counterbalance a high turgor pressure. The author has already reported some preliminary data regarding the rigidity of the wall at the tip (EKDAHL 1948 p. 154). It was shown that in the case of root hairs grown in nutrient solution with sodium chloride ($S + 5.0$ atm.), the hairs had a high osmotic pressure and, if transferred to hypotonic solutions, the growing tip membrane of the hairs could withstand an increase in turgor pressure up to at least 3.5 atm. More exhaustive experiments with roots grown in solutions of varying osmotic strength have confirmed this result and have given about the same value for the turgor pressure increase required to cause a bursting of the tip wall.

Wheat seedlings were grown in S-solutions with sodium chloride added in different amounts to provide a series of solutions with the various osmotic values shown in the head of table 9 (exp. 74). After one to two days' growth in the culture solutions the seedlings were placed in the temperature control cabinet for one to two hours. Before the beginning of the experi-

Table 9. The percentage of growing root hairs plasmoptyzed after the lowering of the osmotic pressure of the culture medium.

Experiment no. 74.

3–4-day-old roots, grown in S+NaCl-solutions, are transferred into culture tubes with S-solutions with hypotonic amounts of sodium chloride. See the text p. 23.

The percentage values are means from three repeated observations and are estimates only.

Osmotic pressure of the hypotonic solution atm.	Osmotic pressure of culture solution atm.			
	5.0+S	4.5+S	4.0+S	3.5+S
	Percentage of plasmoptyzed root hairs			
1.5+S	0			
1.0+S	50–75			
0.5+S	100	0	<25	
S	100	100	100	0

ments a check was made to see that root hairs showed the appearance of normal growth. The seedlings were then quickly transferred into more or less hypotonic solutions, and the reactions of the hairs were observed. Plants from different culture media were used for treatment with the various hypotonic solutions. When the difference between the osmotic values of the two solutions was great, the root hairs burst within a few to ten minutes, but when the difference was small, the tips of the hairs were slowly distended. The details of the immediate reaction of the hairs after the change of solution have already been described (Ekdahl 1948 p. 154). The new results are given in table 9. The values are averages of three experiments and are estimates only. These data once more confirm the old observation (Stiehr 1903) that it is only elongating hairs that burst (*cf.* Ekdahl 1948 p. 155).

Apparently the maximum increase in turgor pressure, which can be withstood by the wall at the tip of the growing hairs, is about 4 atm. Disturbances caused by transferring the plants, however, may influence the reaction of the hairs (*cf.* p. 37). When observed in the observation chamber root hairs burst even if the turgor pressure was increased by 3 atm. only (table 12 p. 29).

When the hairs do not burst, their tips, as mentioned, become more or less distended. The extent of distension varies rather widely with individual hairs and may be related at least in part to differences in the growth rate of the hairs as well as to differences in the rigidity of the walls at the tip, length of the hairs, rate of water absorption, or to differences in the osmotic strength of the external and internal media. In any case, the phenomenon is very complex and involves a great many processes, and it has consequently been

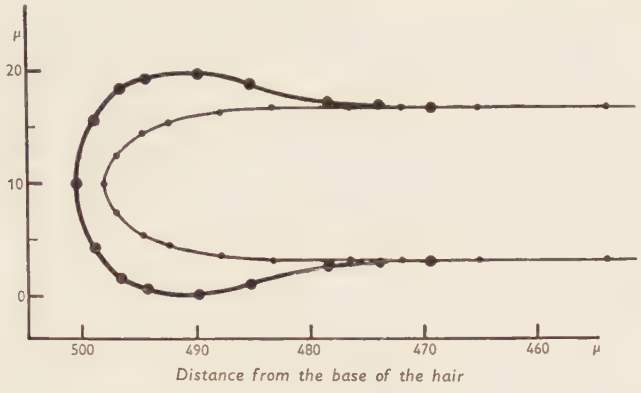

Fig. 1. Root hair apex distended after a lowering of the osmotic pressure of the external medium (increase of the turgor pressure). The medium was changed from $S + 2.5$ atm. NaCl to S-solution, and the distension of the hair was a representative mean. The scheme is drawn with the help of photomicrographs representing the median length-section of a root hair about 500 microns in length. The inner line represents the hair wall just before it began to distend, and the outer line shows the maximum distension after the cessation of elongation. Observe the thickness of the distended wall. See the text pp. 25–27, 38. *Cf.* plate I: fig. 3 and plate II: fig. 11.

found impractical to study all factors influencing the progress and the magnitude of the tip distension. However, in some cases the progress of the distension has been photographically registered until it reached the maximum stage. In fig. 1 some values from such a series of photomicrographs are plotted, the distension of the hair being a representative mean. The registered root hair is from a seedling which was grown in a solution with the osmotic value $S + 2.5$ atm. This solution was then changed into the ordinary S-solution, the interval between the two solutions being 2.5 atm. The hair was about 500 microns in length and the figure gives a scheme drawn with the help of the diameter measured at different distances from the hair tip. The photomicrograph represents the median length-section of the hair, and in the figure the inner line represents the hair wall just before it begins to distend, while the outer line shows the wall after the cessation of the distension, or 70 minutes later.

Figure 1 shows that the hair is stretched only a few microns in the axial direction, but that the diameter of the tip is greatly increased. The extension occurs only within the very tip region less than 25 microns long. The more basal region, most of which is not included in the figure, does not change in diameter. Probably, enlargement ceases gradually from the very tip towards the mature, cylindrical part of the hair as the wall becomes thickened from apposition of wall material. The ratio between the rates of extension of the apical wall and apposition of material in the wall may be important in determining the thickness of the hair wall or the magnitude of

the distension of the hair-tip. In extreme cases the tip does not become distended at all and the wall is immediately stiffened and wall material is sometimes precipitated more or less irregularly in the tip calotte (plate I: fig. 7). The last phenomenon has been observed earlier by several authors (Hopmann 1930; Gorter 1945, 1949 a, b; Lundegårdh 1946; Boysen Jensen 1950) and seems to be one of the reactions of the hairs commonly caused by ceased elongation.

Furthermore, the tips of the hairs become distended also when elongation is interrupted as from vigorous shaking of the roots in the nutrient solution or transferring the plants from one culture tube to another. This effect was noted already by Schwarz (1883), and by many later investigators (earlier literature cited by Ekdahl 1948 p. 121). Also in such cases the distension may be as great as shown in figure 1. Since the osmotic pressure, as well as the chemical composition, of the medium remains unchanged, the distension must be caused by the fact that the formation and the accumulation of osmotically active substances continue after the hair has ceased to elongate (*cf.* Lundegårdh 1946; Ekdahl 1948).

If a root is transferred from a solution to a hypertonic solution the tip will also become distended after the stoppage of elongation. This phenomenon will be more fully elucidated in the next chapter.

8. The growth of root hairs after a lowering of the osmotic pressure of the culture medium.

In the foregoing chapter it has been shown that when the turgor pressure is increased by about 4 atm. the hair tips burst, but when the osmotic changes are less than this, the tips only become distended. If the root hairs are observed for a long time subsequent to the change of medium and when they have begun to distend, it will be found that in some solutions the elongation of the hairs is resumed.

The observations have been made in two types of experiments, one in which the osmotic pressure was varied by the addition of different amounts of sodium chloride to ordinary nutrient solutions, and a second one in which high osmotic pressures were obtained by raising the concentrations of the nutrient salts.

Results of preliminary observations in experiments of the first type are presented in table 10 (exp. no. 75). The roots were grown for 1 to 2 days in ordinary *S*-solutions with sodium chloride added to increase the osmotic pressure by 1–2.5 atm. above the *S*-level, and the roots were then transferred to culture tubes with *S*-solution only (*S* atm.). A few roots from each

Table 10. The growth of root hairs after lowering the osmotic pressure of the culture medium.

Experiment no. 75.

3–4-day-old roots, grown in *S* + NaCl-solutions, are transferred into culture tubes with *S*-solution only (*S* atm.). See the text p. 26.

The values represent 2–3 different observation series.

Osmotic pressure of the culture medium atm.	Growth progress in nutrient solution (*S* atm.)		
	30 min.	60 min.	120 min.
S + 2.5	no growth	no growth	no growth
S + 2.0			
S + 1.5	renewed growth	growth continues	growth continues
S + 1.0	just started		

tube were observed in the microscope at successive time intervals to determine whether the hairs had resumed growth or not. It was found that the hairs did resume growth after having been grown in nutrient solutions with osmotic pressures of *S* + 1.0 to 1.5 atm. and then transferred to the *S*-solution, but they did not resume growth after having been transferred from *S* + 2.0 to 2.5 atm. solutions to *S*-solutions. It must be noted, however, that the elongation of the hairs is disturbed not only by the change in concentration of the medium but also by the transference of the plants from one culture tube into another (*cf.* p. 26). In order to avoid disturbances from the latter cause some experiments (nos. 76–84) were carried out with the roots growing in the observation chamber in which the culture medium could be changed without interruption of the continuous flow of solution. The results are given in tables 11 and 12. As to the arrangements of the experiments, and the methods of calculating the mean values of the elongation rate, "μ/h", and the relation "g/o", see EKDAHL 1948 p. 115.

The experiments show that the hairs elongate at the same rate in an *S*-solution with the osmotic pressure increased by about 2–3 atm. by addition of sodium chloride as they do in pure *S*-solution. The root hairs seem to be well adapted to the culture media used, and the variation of the relation between sodium ions and other cations has no significant effect on the growth rate.

After the change of the flowing medium and the lowering of the osmotic pressure of the solution the root hairs react in two ways. If the difference in osmotic strength between the two media is 1.0 atm., the hairs continue to elongate without interruption. If the difference is 2.0 atm. or more, there is a temporary stoppage of elongation in some hairs. During this latter period

Table 11. The growth rate of root hairs after a lowering of the osmotic pressure of the nutrient solution.

Experiments nos. 76–80.
3–4-day-old roots grown in the observation chamber.
0–120 minutes: *S*-solutions with different amounts of sodium chloride (*S* + NaCl).
120– minutes: *S*-solution (*S*).
Average values in μ/hour, and the relation *g*/*o*, see EKDAHL 1948 p. 115.

Time min.	*S* + 1.0 atm. NaCl ⟶ *S*				*S* + 2.0 atm. NaCl ⟶ *S*					
	76		77		78		79		80	
	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*
	98	6 : 6	**84**	10 : 10	**90**	8 : 8	**80**	11 : 11	**98**	11 : 11
60										
	105	6 : 6	**87**	10 : 10	**94**	8 : 8	**86**	11 : 11	**93**	15 : 15
120										
	78	6 : 6	**67**	7 : 10	**0**	0 : 8	**43**	5 : 11	**38**	10 : 15
	87	6 : 6	**79**	10 : 10	**59**	6 : 8	**61**	10 : 11	**67**	11 : 15
180										
	97	6 : 6	**83**	10 : 10	**75**	6 : 8	**77**	10 : 11	**76**	12 : 15
									81	12 : 15
240										
	97	6 : 6	**81**	10 : 10	**78**	6 : 8	**79**	10 : 11	**82**	12 : 15
300										
			85	10 : 10			**76**	10 : 11	**82**	12 : 15
360										

the apices of the hairs become more or less distended. Fairly soon, however, the hairs adapt to the new solutions and again start to elongate. The rapidity and extent of adaptation after exposure to various lowered osmotic pressures is evident from the data in tables 11 and 12. The values are the means of observations on from 6 to 18 hairs, and, of course, there is some variation in growth recovery between individual hairs in each treatment. In fact, some hairs fail to recover at all. To indicate the degree of variation, values of some individual hairs in experiment 84 are plotted in figure 2 p. 30.

The most important result of the experiments is the fact that the elongation rate of some hairs is rather unaffected by an increase of the turgor pressure, whereas in other hairs both the mode and rate of cell wall growth are immediately changed. After the osmotic pressure of the medium is lowered the root hairs either continue to elongate without interruption and at almost the same rate as before or they completely stop growing for some

Table 12. The growth rate of root hairs after a lowering of the osmotic pressure of the nutrient solution.

Experiments nos. 81–84.
3–4-day-old roots grown in the observation chamber.
0–120 minutes: *S*-solutions with different amounts of sodium chloride (*S* + NaCl).
120– minutes: *S*-solution (*S*).
Average values in μ/hour, and the relation *g*/*o*, see EKDAHL 1948 p. 115.
Plopt = number of plasmoptyzed root hairs.

Time min.	*S* + 2.5 atm. NaCl ⟶ *S*				*S* + 3.0 atm. NaCl ⟶ *S*					
	81		82		83			84		
	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*	plopt	μ/h	*g*/*o*	plopt
	91	12 : 12	**84**	17 : 17	**86**	12 : 12		**80**	8 : 8	
60										
	94	12 : 12	**82**	18 : 18	**86**	12 : 12		**82**	11 : 11	
120										
	0	0 : 12	**0**	0 : 18	**0**	0 : 12	2	**0**	0 : 11	1
	59	2 : 12	**0**	0 : 18	**0**	0 : 12	2	**0**	0 : 11	1
180										
	69	9 : 12	**43**	10 : 18	**47**	1 : 12	2	**71**	2 : 11	1
	73	9 : 12	**57**	15 : 18	**63**	1 : 12	2	**63**	3 : 11	1
240										
	79	10 : 12	**62**	16 : 18	**55**	2 : 12	2	**68**	3 : 11	1
					67	2 : 12	2			
300										
	81	10 : 12	**56**	14 : 16				**65**	3 : 11	1
360										

time. Furthermore, it has been shown that the hairs adapt to the new solutions very quickly. Thus, following decreases of the osmotic pressure of the medium by 1 to 2 atm. most of the root hairs resume growth very soon, and their original elongation rate is almost completely recovered one to two hours after the medium is changed. Following osmotic pressure decreases of 3 atm., however, only a few hairs resume growth, but these actually attain more than 75 % of their original rates of elongation. In the latter experiments a few hairs burst after the osmotic concentration of the solution was lowered (*cf.* p. 24).

Some experiments were also carried out to determine the growth rate of root hairs in nutrient solutions of different concentrations, and to observe the reaction of the hairs after lowering the concentration of the nutrient salts (exp. nos. 85–98, tables 13–15). Plants were grown in the ordinary *S*-solution as well as in solutions with the concentration increased

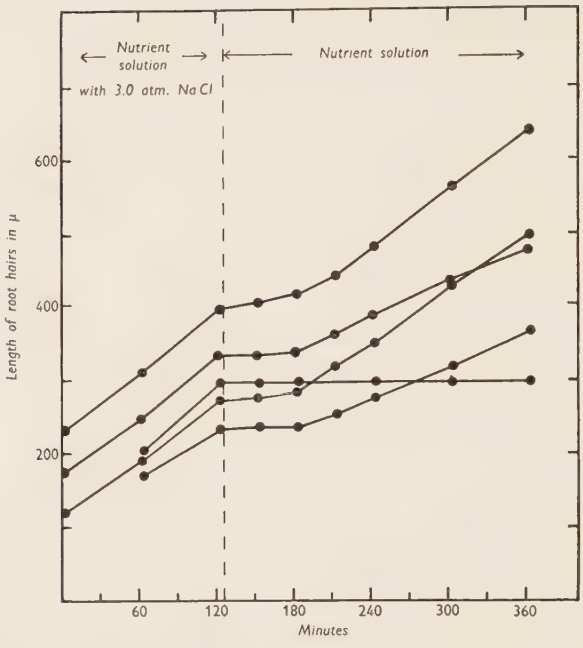

Fig. 2. The growth of root hairs after change of medium from S + 3.0 atm. NaCl to S-solution. Exp. no. 84, table 12.

2.5, 5 or 10 times (2.5 S, 5 S, and 10 S, respectively). In all these solutions the concentrations of iron, manganese, boron, copper and zinc were the same as in the S-solutions. Roots were then taken from the culture tubes and placed in the observation chamber with flowing solution of the same concentration as in the culture tubes but with iron and the trace elements excluded. The growth rate of the hairs was first determined in the latter solutions and then the medium was changed to a less concentrated solution. The solutions with the concentration 10 S, 5 S and 2.5 S were changed to the ordinary nutrient solution (S) (exp. nos. 85–90). In the experiments with the solutions of the latter concentration (S) as the reference medium, the solutions were changed to diluted nutrient solutions with the concentrations $S/2.5$, $S/5$, and $S/10$, respectively (exp. nos. 91–98). The results are given in tables 13–15; they show that the elongation rate of the hairs is the same in nutrient solutions within the concentration range $S/2.5$ to 10 S, and that the lowering of the concentration from 5 S to S or from S to $S/2.5$ has a very slight effect on the average growth rate of the hairs. Some detailed values of experiments 87 and 97 are plotted in figures 3 and 4, p. 33.

It can also be noted that the concentration of the nutrient solution

Table 13. The growth rate of root hairs after a lowering of the concentration of the nutrient salts in the culture medium.

Experiments nos. 85–88.
3–4-day-old roots grown in the observation chamber.
0–120 minutes: nutrient solutions of different concentrations higher than in the ordinary *S*-solution (10 *S* or 5 *S*), the same as in the culture tubes.
120–360 minutes: *S*-solution (*S*).
Average values in μ/hour, and the relation *g*/*o*, see Ekdahl 1948 p. 115.

Time min.	10 *S* → *S*		5 *S* → *S*					
	85		86		87		88	
	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*
	103	2 : 2	**89**	13 : 13	**91**	15 : 15	**83**	9 : 9
60								
	87	9 : 10	**90**	13 : 13	**93**	15 : 15	**88**	9 : 9
120								
	0	0 : 10	**91**	13 : 13	**91**	15 : 15	**89**	9 : 9
180								
	91	10 : 11	**90**	13 : 13	**86**	15 : 15	**88**	9 : 9
240								
	84	10 : 11	**88**	13 : 13	**90**	14 : 15	**85**	9 : 9
300								
	77	9 : 11	**87**	12 : 12	**86**	13 : 15	**82**	9 : 9
360								

seems to limit the growth of the hairs in the most dilute solutions, *i.e.* *S*/5 and *S*/10. As the pH of all solutions varied only between 6.0 and 6.3, and as the lowering of the osmotic pressure in these experiments with dilute solutions may be considered too small to have an appreciable effect, it seems difficult to find out what is responsible for the decreased growth rate of the hairs. This decrease in rate occurs gradually and first in the most dilute solutions. The apices of the hairs never become distended, which indicates that the growth mechanism has not been subjected to any abrupt disturbances. These observations are in accordance with those of Lundegårdh (1946), who studied some growth reactions of root hairs of wheat seedlings and always used the elongation rate in distilled water as a standard. With this medium Lundegårdh found that the hairs elongated at a constant rate for at least 1 to 2 hours, but the rate was only 30 to 50 microns per hour at 22 to 23° C. The author has found a mean rate of about 90 microns per

Table 14. The growth rate of root hairs after a lowering of the concentration of the nutrient salts in the culture medium.

Experiments nos. 89–93.
3–4-day-old roots grown in the observation chamber.
0–120 minutes: nutrient solutions of different concentrations (2.5 *S* or *S*).
120–360 minutes: nutrient solutions with lower concentration than in the culture medium (*S* or *S*/2.5).
Average values in μ/hour, and the relation *g*/*o*, see Ekdahl 1948 p. 115.

Time min.	2.5 *S* → *S*				*S* → *S*/2.5					
	89		90		91		92		93	
	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*
60	**88**	10 : 10	**82**	11 : 11	**86**	12 : 12	**81**	15 : 15	**87**	13 : 13
120	**93**	11 : 11	**86**	13 : 13	**89**	12 : 12	**80**	15 : 15	**92**	14 : 14
180	**93**	13 : 14	**88**	13 : 13	**81**	12 : 12	**81**	13 : 15	**90**	14 : 14
240	**92**	13 : 14	**86**	13 : 13	**89**	12 : 12	**76**	13 : 15	**91**	14 : 14
300	**92**	13 : 14	**87**	13 : 13	**89**	12 : 12	**79**	13 : 15	**88**	13 : 14
360	**91**	13 : 14	**85**	13 : 13	**87**	12 : 12	**78**	13 : 15	**89**	13 : 14

hour in the ordinary *S*-solution at 20 to 21° C (Ekdahl 1948 p. 119) and from the experiments presented in this paper the average value of the elongation rate was found to be 87 μ/hour during the first period (0–60 min.) and 90 μ/hour during the second period (60–120 min.). About the same value was found by Kopp (1948) who made her observations at the same time and in a similar manner as the author.

In all these cases the shape of the hairs was the same. Characteristically, especially the elongating hairs had conical tips (fig. 1, p. 25; *cf.* Lundegårdh 1946 fig. 7; Kopp 1948 plate 2: fig. 1; Ekdahl 1948 plate XI: fig. B). However, if the plants are grown in the dilute *S*-solutions (*S*/5 and *S*/10) for one or more days the roots and root hairs seem to have become adapted to the low nutrient concentration. The elongatiog rate of root hairs from plants grown in *S*-solutions diluted 5 or 10 times were studied in the observation chamber (exp. nos. 99–102, table 16). It is striking that the hairs elongate

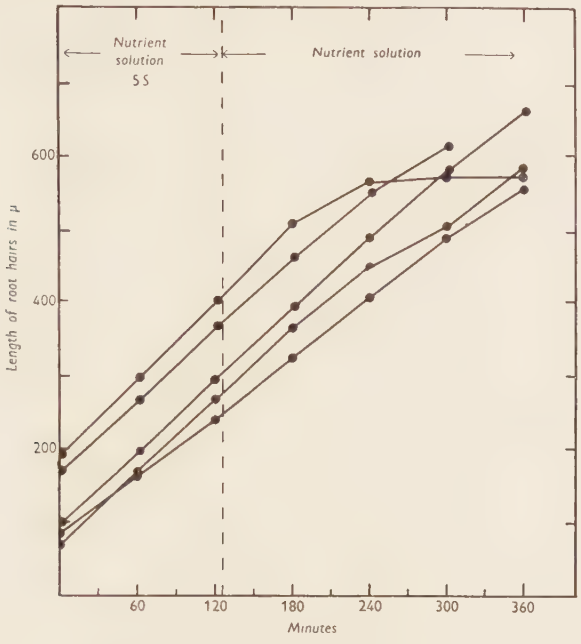

Fig. 3. The growth of root hairs after change of medium from 5 *S*-solution to *S*-solution. Exp. no. 87, table 13.

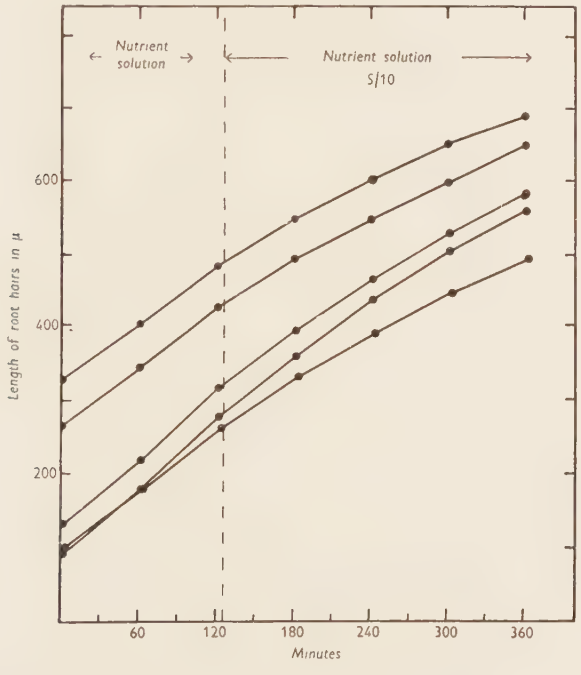

Fig. 4. The growth of root hairs after change of medium from *S*-solution to *S*/10-solution. Exp. no. 96, table 15.

Table 15. The growth rate of root hairs after a lowering of the concentration of the nutrient salts in the culture medium.

Experiments nos. 94–98.
3–4-day-old roots grown in the observation chamber.
0–120 minutes: *S*-solution (*S*).
120–360 minutes: nutrient solutions with lower concentrations than in the ordinary *S*-solution (*S*/5 or *S*/10).
Average values in μ/hour, and the relation *g*/*o*, see Ekdahl 1948 p. 115.

Time min.	*S* ⟶ *S*/5				*S* ⟶ *S*/10					
	94		95		96		97		98	
	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*
60	**87**	11 : 11	**86**	13 : 13	**85**	8 : 8	**81**	11 : 11	**90**	10 : 10
120	**93**	11 : 11	**89**	13 : 13	**91**	8 : 8	**86**	11 : 11	**97**	10 : 10
180	**81**	11 : 11	**85**	13 : 13	**75**	8 : 8	**72**	11 : 11	**78**	10 : 10
240	**70**	11 : 11	**78**	13 : 13	**63**	8 : 8	**60**	11 : 11	**72**	10 : 10
300	**65**	11 : 11	**69**	13 : 13	**48**	8 : 8	**56**	11 : 11	**53**	9 : 10
360	**57**	10 : 11	**62**	13 : 13	**39**	8 : 8	**50**	11 : 11	**51**	9 : 10

at about the same rate in these dilute as in undiluted *S*-solutions or in more concentrated nutrient solutions. The decrease found in experiments 94–98 may be due to the fact that the root hairs grown in the more concentrated solutions are adapted to higher external nutrient concentrations than are the hairs grown in lower concentrations. Following the change in medium, the effect of the concentration difference between the original culture solution and the solution in the observation chamber seems to be less favourable the more dilute the original solution has been.

Furthermore, measurements of the hairs on roots grown in nutrient solutions of different concentrations have shown that the growth and the development of root hairs is almost the same in ordinary *S*-solution as in this solution diluted 5 times (exp. nos. 103–104, table 17). Only in solutions diluted 25 times or more does the initiation as well as the development of the hairs seem to be altered. No concentration between *S*/5 and *S*/25 has been tested. Thus, it seems as if root hairs initiated and developed in the

Table 16. The growth rate of root hairs in diluted nutrient solutions.

Experiments nos. 99–102.

3–4-day-old roots grown in the observation chamber in the same diluted *S*-solutions as in the culture tubes.

Average values in μ/hour, and the relation *g*/*o*, see Ekdahl 1948 p. 115.

Time min.	*S*/5				*S*/10			
	99		100		101		102	
	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*
	85	13 : 13	**83**	10 : 10	**86**	11 : 11	**79**	14 : 14
60								
	89	13 : 13	**90**	11 : 11	**85**	11 : 11	**82**	14 : 14
120								
	90	13 : 13	**89**	11 : 11	**81**	11 : 11	**80**	13 : 14
180								
	87	13 : 13	**91**	11 : 11	**87**	11 : 11	**78**	13 : 14
240								
	86	13 : 13			**82**	11 : 11	**76**	13 : 14
300								

S-solution diluted 5 to 10 times are adapted to the dilute medium and can reach the same elongation rate as in the undiluted *S*-solution.

As a comparison two experimental series were made with pure calcium chloride solutions as a medium (exp. nos. 105–106, table 18). It is shown that also in this medium the roots develop almost as well as in the nutrient solutions. Even root hairs developed abundantly but they did not elongate to the same extent as in the nutrient solutions.

From the results it can be concluded that the elongation rate of the root hairs is influenced only slightly by the concentration of the nutrient salts in the culture medium. Within the concentration range 10 *S* to *S*/10 the growth rate is found to be almost constant, and only in still more dilute solutions does the concentration of the medium seem to become a limiting factor in the process of hair elongation.

The root hairs have a high turgor pressure. Although their walls must be very thin at the growing tip, which is continuously stretched during the elongation, they must be very resistant and have a high ability to withstand high pressures. The experiments show that an increase of the turgor pressure of the growing hairs does not increase their elongation rate which, in fact, seems to be practically independent of any increase in turgor pressure up to the point where it inhibits elongation completely.

Table 17. The development of root hairs in nutrient solutions of different concentrations.

Experiments nos. 103–104.
6-day-old roots. See the text p. 34.
Fresh weight: mean values from 6 groups of 14 plants.
Root-hair-free zone: mean values from 13 roots.
Root hair length: mean values from 9 roots.

Medium conc., parts of *S*-solution	Fresh weight of roots from 14 plants g	Length of root tip free from root hairs mm	Average length of root hairs in μ at different distances (mm) from the root tip				
			5	10	20	30	40
1 : 1	0.88	6.4	0	140	740	1 300	1 450
1 : 5	0.94	6.3	0	155	600	1 250	1 400
1 : 25	0.76	4.8	40	270	550	950	1 100
1 : 125	0.78	4.1	55	105	165	250	325
1 : 625	0.63	3.2	85	90	120	175	

Table 18. The development of root hairs in solutions with different concentrations of calcium chloride.

Experiments nos. 105–106.
6-day-old roots. See the text p. 35.
Fresh weight: mean values from 6 groups of 14 plants.
Root-hair-free zone: mean values from 13 roots.
Root hair length: mean values from 9 roots.

Medium conc., parts of $CaCl_2$ $M/1\,000$	Fresh weight of roots from 14 plants g	Length of root tip free from root hairs mm	Average length of root hairs in μ at different distances (mm) from the root tip				
			5	10	20	30	40
1 : 1	0.89	6.3	0	145	290	700	575
1 : 5	0.88	6.3	0	60	190	290	340
1 : 25	0.76	4.7	30	90	160	160	325
1 : 125	0.69	3.9	30	50	95	110	140
1 : 625	0.58	2.1	25	40	95	110	

9. The growth of root hairs after an increase of the osmotic pressure of the culture medium.

The root hair tips distend not only after mechanical disturbances (*cf.* EKDAHL 1948 p. 121) or after increases in their turgor pressure but also in some cases if the hairs are transferred to salt solutions hypertonic to their nutrient solution, *i.e.* after a lowering of the turgor pressure. Under these conditions the hairs burst even in some salt or sugar solutions.

The reaction of root hairs after transference to salt solutions has been carefully studied by STIEHR (1903). He found that solutions of some inorganic salts in concentrations of 0.1 to 0.5 per cent may cause a plasmoptysis of root hairs of young *Phleum* seedlings. Those hairs, which were not plasmoptyzed, became distended at their tips as did hairs in solutions of less than 0.1 per cent. As the phenomenon of plasmoptysis is of great interest to our understanding of the growth mechanism of root hairs, the author has thought it worth repeating STIEHR's experiments on wheat plants.

This part of the investigation concerns the influences on the root hairs of wheat seedlings of pure sodium chloride solutions or of *S*-solutions with sodium chloride. Some observations have also been made with potassium, calcium, or glucose solutions as a medium.

The effects of increased strength of the medium on the root hairs have been studied in two different series. In the first series the progress of the plasmoptysis and distension of the hair tips has been observed, and in the second one determinations were made of the rates of elongation of the hairs in the salt solutions.

In the first series 3–4-day-old seedlings in cork-holders were rapidly transferred from the ordinary *S*-solution into new culture tubes with the salt solutions to be tested. One-half to two hours later the root hairs on 6 to 12 roots from each tube were observed in the microscope. This method, which is comparable to that of STIEHR, makes it possible to test a great number of solutions at one and the same time and with the same, uniform plant material. This is of very great importance as there may be small differences from day to day in several internal factors regulating the reaction of the hairs, factors which are not subject to experimental control. On the other hand, disturbances caused by transferring the plants cannot be avoided by this method. Thus, the numerical values obtained by this method are not quantitatively exact, but they clearly show the general nature and trends of the reactions of the hairs.

The elongation rate of the hairs is one property of the cell which seems to regulate the hair reaction and the frequency of plasmoptysis. Thus, rapidly growing hairs, on an average, burst more often than slowly growing hairs (see table 25, p. 45), and hairs that are not elongating do not burst at all (*cf.* p. 24, and STIEHR 1903 p. 48).

The first two experimental series with this method were carried out, one in February (exp. no. 107) and another in November 1950 (exp. nos. 108–109), to determine the effect of pure sodium chloride solutions. The same seed material, culture conditions, and similar solutions were used in both series. Essentially, the results from these two series are the same (table 19), but they differ in some details (tables 20–22).

Table 19. Reaction of root hairs after transference into pure sodium chloride solutions.

Data summarized from experiments no. 107, February 1950, and nos. 108, 109, November 1950.

Medium conc., *M* NaCl	Osmotic pressure of the medium atm.	Reaction of the hairs		
		distension of the tips	resumed growth	plasmoptysis
0.01	0.5	+	+	0
0.03	1.4	+	+	+
0.05	2.3	+	+	+
0.08	3.6	+	+	+
0.10	4.5	+	0	+
0.12	5.4	0	0	+
0.14	6.3	0	0	+
0.16	7.2	0	0	0

It is evident from both series that *the hair tips distended* in pure sodium chloride solutions of concentrations up to 0.10 *M*. The osmotic pressure of 0.10 *M* NaCl-solution is about 4.5 atm. at 20° C, and, as the hairs have an osmotic pressure of about 7.5 atm., the turgor pressure of the hairs has been lowered to about 3 atm. Nevertheless, the hair tips distend.

Resumed growth from distended tips was observed only in solutions with concentrations from 0.01 to 0.08 *M* NaCl. The elongation was resumed more rapidly in the more dilute solutions (*cf.* exp. nos. 120–124, tables 24–25, plate I: figs. 4 and 5).

Plasmoptysis of root hairs has been observed in the concentration range from 0.03 to 0.14 *M* NaCl. The detailed results, however, are not quite the same for both series. The 0.14 *M* solution caused plasmoptysis in February (exp. no. 107, table 20) but only in one of the experiments in November (exp. no. 109, table 22). By contrast, the 0.03 *M* solution caused plasmoptysis in November (exp. nos. 108–109, tables 21–22) and not in February. In February hairs up to 500 microns in length burst, and maximally 50 per cent of the hairs were observed to be plasmoptyzed. On the other hand, the observations made in November show that the hairs did not burst so frequently, and further, that mostly the short hairs, not longer than 200 microns, were plasmoptyzed (tables 21 and 22). The differences between the two series are, however, so small that they cannot be taken as a proof of seasonal variations.

The root hairs show plasmoptysis already between a few to ten minutes after transference to the sodium chloride solutions (*cf.* Ekdahl 1948). The

Table 20. Plasmoptysis and plasmolysis of root hairs after transference into pure sodium chloride solutions.

Experiment no. 107, February 1950.
3–4-day-old roots. See the text p. 37.
Each value is the mean for 30–36 roots.
The per cent values of plasmoptyzed hairs are estimates only.

Medium conc., *M* NaCl	Osmotic pressure of the medium atm.	Per cent of roots showing		Plasmoptyzed root hairs in per cent (hairs < 500 μ)		
		Plasmoptysis	Plasmolysis			
		A+B+C	A+B+C	A	B	C
0.01	0.5	0				
0.03	1.4	0				
0.05	2.3	42		5	5	5
0.08	3.6	56		15	15	25
0.10	4.5	69		10	20	25
0.12	5.4	50		5	10	10
0.14	6.3	14		0	5	5
0.16	7.2	0	0			
0.18	8.1		75			
0.20	9.0		100			
0.22	9.8		100			

turgor pressure of the hairs was lowered by 1.4 to 6.3 atm. after the transference to the sodium chloride solutions. Nevertheless, the hair tips burst. This bursting in pure sodium chloride solutions seems to indicate that the tensile strength of the growing apical wall is lowered by the sodium salt. It seems improbable that an active accumulation of sodium and chloride ions in the hairs could increase their turgor pressure so rapidly as to overcome the high tensile strength of the normal apical wall.

In 0.18 *M* and stronger NaCl-solutions 50 per cent or more of all growing hairs were *plasmolyzed* (*cf.* p. 20).

Stiehr (1903 p. 27 and 49) put forward the theory that the bursting of the hairs in salt solutions was caused by disturbances in the formation of new wall material and, as a result, a weakening of the tip membrane. Furthermore, he considered it improbable that the salt solutions could change the structure or the composition of the existing cell wall.

Now it is a well-known fact, however, that calcium ions, more than other essential ions, are promoting the growth of roots of higher plants (Hansteen 1910, Hansteen Cranner 1914; Brenner 1920; Trelease and Trelease 1925, 1926; Mevius 1927; Lundegårdh 1932, 1949 b; Burström 1934, 1952). Furthermore, through the exhaustive investigations of Lunde-

Table 21. Plasmoptysis of root hairs after transference into pure sodium chloride solutions (NaCl) or into nutrient solutions with sodium chloride (S + NaCl).

Experiment no. 108, November 1950.
3–4-day-old roots. See the text p. 37.
Each value is the mean for 30–48 roots.
The per cent values of plasmoptyzed hairs are estimates only.
The concentrations of NaCl in the S + NaCl-solutions are isotonic to those of the corresponding pure NaCl-solutions.

Medium conc., M NaCl	Osmotic pressure of the medium atm.	Per cent of roots with plasmoptyzed hairs		Plasmoptyzed root hairs in per cent (hairs < 200 μ)	
		NaCl	S + NaCl	NaCl	S + NaCl
0.01	0.5	0	0		
0.03	1.4	4	16	<5	<5
0.05	2.3	44	40	5–10	5–10
0.08	3.6	63	50	10–20	5–10
0.10	4.5	57	25	10–20	5–10
0.12	5.4	22	8	<5	<5
0.14	6.3	0	0		
0.16	7.2	0	0		

GÅRDH (1940, 1943, 1945) it has been shown that the cytoplasmic membrane of the root epidermal cells, as well as of root hairs, can be looked upon as a thin surface built up by an amphoteric colloid with preferable acidic dissociation. The electrical charge of the membrane and the amount of cations adsorbed to the surface can be highly changed by altering the composition of the external medium (LUNDEGÅRDH 1938, 1941, 1942). Cations are also incorporated in the cell wall and anions are used in the formation of organic constituents of the cytoplasm and its membranes. The plasmoptysis effects of sodium chloride and other salts observed could, thus, probably be caused by changes of the chemical or the physical properties of the cell wall as well as of the cytoplasm and its membranes. Therefore, it seemed valuable to make a more detailed study of the plasmoptysis effects of sodium ions and other cations, especially of calcium, and to examine to what extent the progress of the plasmoptysis can be changed by variations of the ions and their concentration in the plasmolyzing solutions. Consequently, the following experiments were carried out.

In the first experiment the effects of the same sodium chloride concentrations as were used earlier (see table 19) were tested with and without the presence of the nutrient salts of the ordinary S-solution (exp. no. 108, table

Table 22. Plasmoptysis of root hairs after transference into pure sodium chloride solutions (NaCl), nutrient solutions with sodium chloride and the amount of calcium nitrate increased three times ($S + 2\,Ca + NaCl$), glucose solutions or into nutrient solutions with glucose.

Experiments nos. 109–110, November 1950.
3–4-day-old roots. See the text p. 37.
Each value is the mean for 18–36 roots.
The per cent values of plasmoptyzed hairs are estimates only.
The glucose solutions are isotonic to the sodium chloride solutions.

Medium conc., *M* NaCl	Osmotic pressure of the medium atm.	Per cent of roots with plasmoptyzed hairs (< 200 μ)			
		109		110	
		NaCl	$S + 2Ca + NaCl$	Glucose	S + glucose
0.01	0.5	0	0	0	0
0.03	1.4	25	0	0	0
0.05	2.3	42	0	0	8
0.08	3.6	92	8	33	17
0.10	4.5	75	17	50	0
0.12	5.4	67	0	25	0
0.14	6.3	33	0	8	
0.16	7.2	0		0	

21). The entire concentration series was tested four times and the results show that the addition of the nutrient salts lowered the frequency of plasmoptysis in the roots as well as in the hairs of the individual roots (table 21). Comparisons were also made between the effects of the pure NaCl-solutions and those of ordinary *S*-solutions with the standard amount of calcium nitrate increased three times and with the different amounts of NaCl (S + 2 Ca + NaCl, exp. no. 109, table 22). In other experiments the pure NaCl-solutions were compared with combinations of NaCl and three or four times the amount of nutrient salts (NaCl + 3 *S* and 4 *S*, respectively, exp. nos. 111–112, table 23) or only four or ten times the standard amount of $Ca(NO_3)_2$ (NaCl + 4 Ca and 10 Ca, respectively, exp. nos. 113–114, table 23). Finally, combinations with NaCl-solutions and 0.01 *M* $CaCl_2$ were tested (exp. no. 115, table 23). In the experiments nos. 111–115 the frequencies of plasmoptysis were observed in 0.08, 0.10 and 0.12 *M* NaCl-solutions and the combinations with these solutions. The observation series were repeated two times only. All the experiments (nos. 109–115) show that the additions of the nutrient salts or the different amounts of pure calcium salts lower or inhibit the plasmoptysis effect of the NaCl-solutions.

It has been shown that root hairs burst in sodium chloride solutions with

Table 23. The reaction of root hairs in different salt and glucose solutions hypertonic to the ordinary nutrient solution.

Exp. nos. **111–115**: the frequencies of plasmoptysis are referred to observations of the effects of 0.08, 0.10 and 0.12 *M* NaCl-solutions and the combinations with these solutions.

Exp. no. **116**: 0.08, 0.10 and 0.12 *M* KCl-solutions have been compared with NaCl-solutions of corresponding concentrations.

Exp. no. **117**: the frequency of plasmoptysis is referred to observations of the effects of 0.01–0.08 *M* $CaCl_2$-solutions.

Exp. no. **118**: the frequency of plasmoptysis is referred to observations of the effects of 0.01–0.08 *M* $Ca(NO_3)_2$-solutions.

Exp. no. **110**: the glucose solutions have been isotonic to 0.01–0.16 *M* NaCl-solutions.

+ + + = plasmoptysis resp. distension frequent.
+ + = » » » less frequent.
+ = » » » infrequent.
– = no plasmoptysis resp. distension.
(+) = plasmoptysis of very short hairs only (< 50 μ).

Experiment No.	Medium	Reaction of the hairs	
		plasmoptysis	distension
111–115	NaCl	+ + +	+ + +
111	NaCl + 3 *S*	+	+ +
112	NaCl + 4 *S*	–	+ +
113	NaCl + 4 Ca	+	+ +
114	NaCl + 10 Ca	–	+
115	NaCl + 0.01 *M* $CaCl_2$	–	–
116	KCl	+ + +	+ + +
117	0.01–0.10 *M* $CaCl_2$	(+)	+
118	0.01–0.10 *M* $Ca(NO_3)_2$	(+)	+
110	Glucose	+ +	+ +
110	Glucose + *S*	+	+

a concentration hypertonic to the ordinary *S*-solution. Further, the bursting of the hairs in sodium chloride can be lowered or inhibited by an addition of the complete *S*-solution or by calcium salts alone. These facts seem to support the interpretation that the sodium chloride changes the tip membrane through an exchange of cations, especially calcium. Instead of insoluble calcium pectate there may be formed soluble sodium pectate, or organic molecules connected with each other in chains by the bivalent calcium ions will be loosened. Stiehr (1903), however, found that root hairs burst even in solutions of pure calcium nitrate.

In order to recapitulate Stiehr's observations some experiments were carried out to elucidate the effects of pure calcium chloride, calcium nitrate

and potassium chloride solutions on the root hairs. The observations, made after transference of the roots from the ordinary *S*-solutions to solutions of the pure salts, only partly confirm STIEHR's results. The concentration range of the tested solutions was 0.01 to 0.10 *M*, the intervals in the solution series being 0.02 *M* of the salts used. The results from some observations are given in table 23. The potassium solutions have almost the same effects as corresponding sodium solutions (exp. no. 116). The plasmoptysis in the calcium solutions (exp. nos. 117–118), although quite evident, was always somewhat irregular, and, most significantly, only the very short hairs (< 50 microns in length) did burst. Longer hairs only showed distended tips. The differences between the mode of plasmoptysis in sodium or potassium solutions and that in the calcium solutions were so evident that it must be concluded that the calcium ions influence the thin growing membranes of the hair tips in quite another manner than do the sodium or the potassium ions.

Lastly, glucose solutions, isotonic to the NaCl-solutions, were tested to observe the effects of an increase in the osmotic pressure of the medium by an undissociated substance. The hairs proved to burst in glucose solutions isotonic to from 0.08 to 0.12 *M* NaCl. Furthermore, the frequency of plasmoptysis in glucose solutions could be lowered by an addition of the nutrient salts (exp. no. 110, tables 22 and 23).

In a second series of experiments concerning the effects of increased osmotic pressure of the medium, flowing solutions were tested on roots growing in the observation chamber (see p. 9). This arrangement gives as small changes in the external conditions as possible. In this case it is possible to determine the growth rate of the hairs before as well as after the change of solution. However, it is too laborious to make detailed observations of the effects of all solutions on single hairs in a sufficiently great number to get adequate mean values of the percentage of plasmoptyzed root hairs.

This method, however, has been used for studies of the progress of the elongation of the hairs following increases in osmotic pressure of the medium, *i.e.* a lowering of the turgor pressure of the cells. The results are given in tables 24 and 25 (exp. nos. 119–124). It is shown that increases of the osmotic pressure of the flowing nutrient solution by addition of concentrations of 2.0 atm. NaCl either lowered the growth of the hairs or caused an immediate inhibition of their elongation. The inhibition of the growth of the hairs is more frequent in the $S + 2.5$ atm. NaCl-solution than in the less concentrated solutions. On root hairs with ceased growth the hair tips were more or less distended. The growth is, however, very soon resumed. After changes from *S*-solution to $S + 2.0$ atm. NaCl-solution almost all the hairs resumed their elongation within 30 minutes. During the subsequent

Table 24. The growth of root hairs after increase of the osmotic pressure of the nutrient solution.

Experiment no. 119.
3–4-day-old roots grown in the observation chamber.
0–120 minutes: *S*-solution (*S* atm.).
120–300 minutes: *S*-solution with 2.0 atm. sodium chloride (*S* + 2.0 atm. NaCl).
300–540 minutes: *S*-solution (*S* atm.).
Experiments nos. 120–121.
3–4-day-old roots grown in the observation chamber.
0–120 minutes: *S*-solution (*S* atm.).
120–360 minutes: *S*-solution with 2.0 atm. sodium chloride (*S* + 2.0 atm. NaCl).
Average values in μ/hour, and the relation *g*/*o*, see Ekdahl 1948 p. 115.

Time min.	*S* ⟶ *S* + 2.0 atm. NaCl *S* + 2.0 atm. NaCl ⟶ *S*		*S* ⟶ *S* + 2.0 atm. NaCl			
	119		120		121	
	μ/h	*g*/*o*	μ/h	*g*/*o*	μ/h	*g*/*o*
	90	8 : 8	**81**	11 : 11	**93**	14 : 14
60						
	88	8 : 8	**85**	11 : 11	**97**	14 : 14
120						
	37	6 : 8	**0**	0 : 11	**0**	0 : 14
	71	8 : 8	**55**	11 : 11	**75**	9 : 14
180						
	70	7 : 8	**79**	11 : 11	**83**	11 : 14
240						
	61	6 : 8	**82**	11 : 11	**87**	11 : 14
300						
	0	0 : 8	**79**	11 : 11	**85**	11 : 14
360						
	42	3 : 8				
420						
	40[1] **74**[2]	3 : 8 7 : 7				
480						
	34 **78**	2 : 8 7 : 7				
540						

[1] 420 min. — length of root hairs = 500–800 μ.

[2] 420 min. — root hairs initiated in the *S* + 2.0 atm. NaCl-solution; length of root hairs = 100–200 μ.

3–4 hours' period the hairs elongated at the rate of more than 75 per cent of the reference value (table 24, exp. nos. 120–121). The osmotic pressure of the medium was increased from *S* to *S* + 2.5 atm. NaCl in only one experiment (exp. no. 122, table 25), and root hairs from two roots, placed side by side in the observation chamber, were observed. In the ordinary *S*-solu-

Table 25. The growth of root hairs after the increase of the osmotic pressure of the nutrient solution.

Experiments nos. 122-124.
3–4-day-old roots grown in the observation chamber.
0–120 minutes: *S*-solution (*S* atm.).
120– minutes: *S*-solution with different amounts of sodium chloride (*S* + NaCl).
Average values in μ/hour, and the relation *g*/*o*, see EKDAHL 1948 p. 115.
Plopt = number of plasmoptyzed hairs.

Time min.	*S* ⟶ *S* + 2.5 atm. NaCl						*S* ⟶ *S* + 3.0 atm. NaCl				
	122						123			124	
	root A			root B							
	μ/h	*g*/*o*	plopt	μ/h	*g*/*o*	plopt	μ/h	*g*/*o*	plopt	μ/h	*g*/*o*
	73	8 : 8		**86**	9 : 9		**93**	13 : 13		**88**	11 : 11
60											
	75	8 : 8		**89**	9 : 9		**95**	13 : 13		**92**	12 : 12
120											
	0	0 : 8	0	**39**	3 : 9	3	**0**	0 : 13	13[1]	**0**	0 : 12
	56	5 : 8	0	**76**	5 : 9	3	**0**	0 : 13	13	**0**	0 : 12
180											
	54	5 : 8	0	**84**	6 : 9	2	**0**	0 : 13	13	**75**	5 : 12
	54	5 : 8	0	**86**	6 : 9	2	**0**			**83**	7 : 12
240											
	52	5 : 8	0	**87**	6 : 9	2				**85**	7 : 12
300											
	51	5 : 8	0	**80**	6 : 9	2				**83**	7 : 12
360											

[1] Root hairs on the opposite side of the root did not burst at all, their growth rate was not determined.

tion the hairs on one of the roots (A) grew at the rate of 73 to 75 μ/hour, but the hairs on the other root (B) at a more rapid rate, 86 to 89 μ/hour. After the change of medium from *S* to *S* + 2.5 atm. NaCl, the root hairs reacted in very different ways; some of them continued to grow without interruption, others were plasmoptyzed, and most of them stopped growing. On root B, with hairs of the highest mean rate of elongation, three of the observed hairs continued to grow at the rate of about half the value of the ordinary rate, three hairs burst within ten minutes, and the other three hairs observed ceased to grow for a short time and their tips began to distend. Soon afterwards, however, the walls in a small area at the very tips of these latter hairs were thinned out and the hairs resumed their growth. Even in

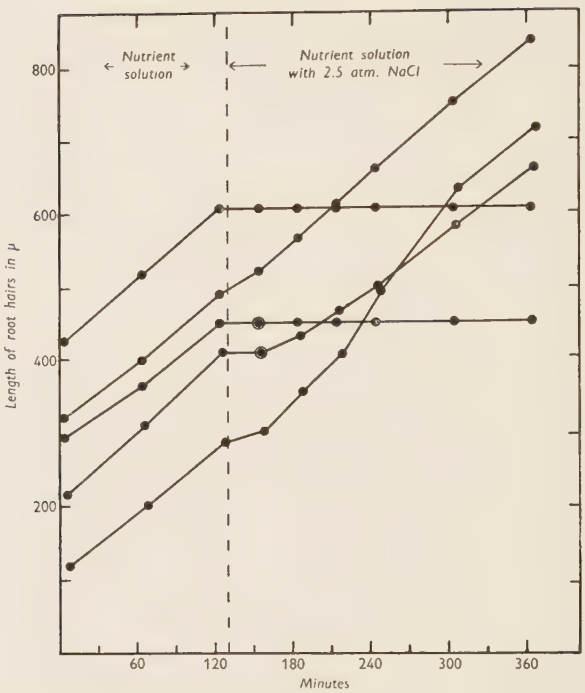

Fig. 5. The growth of root hairs after change of medium from S-solution to S + 2.5 atm. NaCl. Exp. no. 122, root B, table 24. ⊙ = the root hair is plasmoptyzed.

this solution the hairs recovered a growth rate of about 75 per cent of the control value. One of the plasmoptyzed hairs of root B soon began to grow again and at about the same elongation rate as the other hairs, and after 2 hours its elongation rate was about the same as the mean rate of the other hairs (table 25, fig. 5; *cf.* plate I: fig. 6, and EKDAHL 1948 p. 115 and plate I: fig. C). Similarly, KERR (1933) found that root hairs of *Limonium spongia* burst after injections of solutions of NaCl and other salts into the hair vacuoles and that growth recovery frequently followed. All the hairs observed on root A stopped growing after the change of medium. One hour later, however, also these hairs had resumed growth, but they had not recovered the same high growing rate as the hairs on root B. In experiments nos. 123 and 124 the S-solution was replaced by an S + 3.0 atm. NaCl-solution. In exp. no. 123 the hairs elongated rather rapidly, 93 to 95 μ/hour. After the change of the flowing solution all observed hairs burst within ten minutes and none of the hairs elongated afterwards. It should be mentioned, however, that some hairs on the opposite side of one of the roots did not burst, and later a few of them resumed growth.

In experiment no. 124 the increase of the osmotic pressure of the medium,

from S to $S + 3.0$ atm. NaCl, did not cause any plasmoptysis at all, but the root hairs stopped elongating and their tips were distended. One hour after the change of medium, however, about half of the observed hairs resumed growth and the recovery was almost complete.

In the last experiments, in which the flowing medium in the observation chamber was changed from a mere S-solution to S-solutions with the osmotic pressure increased by addition of sodium chloride (S + 1.0 to 3.0 atm. NaCl), it appears that the hairs react very differently. It is obvious, however, that root hairs can elongate undisturbed by the change of medium, but at a lowered rate, even if the difference between the media is as high as 2.5 atmospheres. In the same experiment and on the same root some hairs continued to grow without any interruption, whereas other hairs stopped elongating completely, or after high increases of the osmotic pressure of the medium some other hairs were plasmoptyzed. It may be supposed that it is not the change of the osmotic pressure that is primarily the cause of the stoppage of growth or the plasmoptysis of the hairs but that the rapidity, at which the exchange of ions between the protoplasmic membranes of the epidermal cells and the hairs and the surrounding medium takes place, may be of great importance in this case. LUNDEGÅRDH (1940, 1941, 1942) has shown that an addition of salts to the medium can greatly change the electrical charge of the root and the root hair surfaces, and this change is caused by an exchange of ions between the medium and the protoplasmic membranes of the epidermal cells and the root hairs. There is not yet any explanation why some hairs burst, others stop to grow for a short or long time and others elongate quite unaffected of the change of medium.

The observation of undisturbed elongation in even highly concentrated solutions is in good agreement with LUNDEGÅRDH's results (1946). He found that root hairs of wheat seedlings elongated at an unaffected or slightly accelerated rate in solutions of 0.04 to 0.10 M glucose. From LUNDEGÅRDH's and my own experiments it may be concluded that the elongation rate of root hairs may not be influenced primarily by changes of the turgor pressure of the hairs.

The results from experiments in this and the previous chapter have given good evidence of the great ability of the root hairs to overcome differences of the osmotic pressure of the surrounding medium.

10. Discussion.

Cell division, cell enlargement and cell differentiation are the three main processes in the growth of plants. Rapid cell elongation, *i.e.* the enlargement of cells preferably in one direction, is one of the conditions for the vigorous

growth of higher plants. During the last two decades comprehensive investigations have been made as to the mechansims of cell elongation and the processes regulating cell enlargement.

In primary cell walls (see KERR and BAILEY 1934 p. 342) the growth in surface is the dominant process whereas the growth of secondary cell walls mostly comprises a thickening of the walls. The growth in surface of cell walls has been the subject of several investigations concerning cell elongation, and much work has been done to examine the forces which primarily induce the enlargement of the wall surface.

The theories as to the mechanisms of cell elongation and the enlargement of the cell wall surface are surveyed and discussed by SÖDING (1931, 1932, 1952), STRUGGER (1934), CZAJA (1935 a, b), BONNER (1935), FREY-WYSSLING (1935, 1936, 1948 a, b, 1952 a), HEYN (1931 a, b, 1940), RUGE (1942), LUNDEGÅRDH (1942, 1949 a, 1950), BURSTRÖM (1942 a, b, 1951, 1952), and others. Some investigators have suggested that an increase of the turgor pressure of the cells is the primary process causing the stretching of the cell walls, but others have found that an increase of the "plastic" or the "elastic" extensibility of the cell walls is the factor limiting or regulating cell elongation. The arguments adduced for the different theories are extensively discussed by HEYN (1940; see also SÖDING 1952). THIMANN, however, has called attention to the importance of processes in the cytoplasm, which influence the stretching of the primary cell walls (THIMANN and BONNER 1933; THIMANN 1935, 1948 p. 64–65, 1949 a, b, 1951). By analysis of pea seedlings BROWN and BROADBENT (1950) and BROWN (1951; see also BROWN *et al.* 1952) have shown that the increase in size of the cells involves increases in many constituents of the cells. Further, BLANK and FREY-WYSSLING have shown that the amount of cytoplasm is increased during the elongation of cells from different plant organs (BLANK and FREY-WYSSLING 1940, 1941, 1944), and WIRTH (1946) found a considerable increase of the cell wall constituents during the enlargement of the primary walls of the coleoptiles of corn seedlings. From these last data, FREY-WYSSLING (1945, 1948 b) has concluded that the growth in surface of the primary cell walls must be looked upon as an active metabolic phenomenon. This statement is strongly supported by the results from the very exhaustive investigations concerning the effects on cell elongation of auxins and growth regulators that have been carried out during the last ten years (see VAN OVERBEEK 1944; SKOOG 1947, 1951; VELDSTRA and BOOIJ 1949; BONNER and BANDURSKI 1952).

Although we do not know exactly which metabolic processes are directly involved in the growth in surface of primary cell walls or how the responsible processes are linked together to accomplish the net result of cell wall enlargement, we may assume the participation of some vital processes in the cells,

such as processes resulting in free, available energy and processes involved in biosynthesis of cell wall constituents. This growth is then to be regarded as an active process rather than as a passive stretching of the cell wall by the turgor pressure.

Different types of cell enlargement have been distinguished. In stems, roots and other plant organs the growth of tubular cells, mainly in the direction of the long axis of the tissue, is referred to as *elongation growth* or polar growth. KRABBE (1886) assumed that every cell in a tissue grows at its individual rate and that the cell walls of neighbouring cells slide along each other. He called this growth *sliding growth*. Later, however, PRIESTLEY (1930), MEEUSE (1942), and others have shown that the adjacent cell walls in most cases grow at the same rate. This *symplastic growth* (PRIESTLEY 1930 p. 132) presumes that different parts of the wall of one cell can grow at unequal rates. Further, in cases where a cell penetrates into a tissue between two adjacent cells, SINNOTT and BLOCH (1939 b) speak of *intrusive growth*. SCHOCH-BODMER (1945 b) and SCHOCH-BODMER and HUBER (1946) speak of this phenomenon as *interposition growth*. Some specialized cells in which the growth is restricted to a small portion of the area of their walls, *i.e.* to their extreme tips only, are said to exhibit *apical growth*, or *tip growth* (REINHARDT 1892, 1899; SCHOCH-BODMER 1945 a; SCHOCH-BODMER and HUBER 1945 a; and others, see p. 8). In all these cases attention has been paid to the growing cells as elements of living plant tissues. On the basis of the submicroscopic morphology of cell walls, FREY-WYSSLING, however, recently (1948 b) presented a simplification of the terminology, and wants to term all kinds of growth in surface of cell walls as *growth by intussusception*. Maybe, intercalation (intussusception) of wall particles takes place in every type of enlargement of cell wall surfaces, but this growth in surface is only one part of the cell elongation, and we may suggest that the mechanisms by which new particles are intercalated in the wall are different in several details for different plants, tissues or cells. As examples of important processes involved in the meticulously organized mechanism of cell enlargement, the following ones may be mentioned: formation and transport of cell wall and cytoplasm materials as well as osmotically active substances, absorption and movement of salts and water, formation and distribution (uniform or polar) of enzymes and growth regulators. The energy necessary to many of these processes is supplied by respiration. Furthermore, the elongation rate will be dependent on interactions between adjacent cells in the growing tissue, on the composition and structure of their cell walls, and, finally, on the conditions of the external medium which influence most of the processes occurring within the cells.

In the author's opinion it is fairly certain that the mechanism of cell

wall enlargement may vary from tissue to tissue, from cell to cell, and even from one part of a cell to another. Caution must therefore be exercised to avoid false generalizations made on the basis of comparisons between observations from different plant materials. The results obtained from studies of the elongation of cells of *Helianthus* hypocotyles (Gessner 1934; Ruge 1937 a, b; Diehl *et al.* 1939), of *Avena* coleoptiles (Bonner 1935; Heyn 1931 a, b, 1940; Thimann and Bonner 1933; and many others), of turgescent cells of wheat roots (Lundegårdh 1940, 1942, 1949 a; Burström 1941, 1942 a, b, 1951), of *Phycomyces* sporangiophores (Oort and Roelofsen 1932; Castle 1937 a, b, 1940, 1942; Roelofsen 1949; Middlebrook and Preston 1952), of pollen tubes (Schoch-Bodmer 1945 a, Kopp 1948), and of root hairs (Reinhardt 1892; Lundegårdh 1946, Kopp 1948, Ekdahl 1948) seem to be incompatible in many details. As to the role of the turgor pressure as a factor in cell elongation Burström (1942 a) has called attention to the differences in water saturation between roots grown in moist saw dust (*cf.* Ursprung and Blum 1924, 1928) with their incompletely turgid epidermal cells and, on the other hand, fully turgid cells on roots grown in water or dilute nutrient solutions. Heyn (1931 b, 1940) has supposed that the formation of cell wall substances in *Avena* coleoptiles is checked at low temperatures (0 to + 4° C) but that a considerable elongation takes place because the "plasticity" of the cell walls remains rather unaffected. Bonner (1934) also found that the dry weight of the cell walls of *Avena* coleoptiles paralleled the elongation at a temperature of 25° C but that at 0 to + 2° C the cells could elongate without any increase in dry weight of the walls.

Preston and Clark (1944), too, mention that the weight of wall material per length unit of *Avena* coleoptiles decreased almost continually throughout the period of rapid elongation. They found that the weight of wall material per unit length of coleoptiles decreased during the elongation period. The decrease was definitely higher than that calculated with the help of the values of the increased water content of the coleoptiles. The results seem to support the statement that the thickness of cell walls is lowered during the period of rapid elongation, but the analytical method does not permit any definite conclusion. Furthermore, Allsopp and Misra (1940) found that the walls of cambium cells of common ash, common elm and Scotch pine contained much higher amounts of pectic substances and lower amounts of cellulosic substances than did the cell of the new wood. The author has found that soaked wheat seeds placed in moist air in Petri dishes at 0 to + 2° C grew out normally but, of course, at a much slower rate than at 20 to 25° C (table 26). At the low temperature root hairs were formed, too, and they were of an almost normal appearance. These observations show

Table 26. Growth of roots and root hairs of wheat seedlings at low temperatures.

Wheat seeds are soaked and grown in darkness in large Petri dishes in temperature control cabinets. Preliminary results, see the text p. 51.

Temperatur °C	Length of root hairs mm	Length of roots cm	Diameter of roots cm
5–7	2.5	2.3	0.5
0–2	1.9	1.3	0.5

that many of the processes involved in the growth of the cells of roots and coleoptiles of wheat seedlings must take place even at a low temperature. For *Avena* coleoptiles, THIMANN and BONNER (1933) studied the ratio between the number of auxin molecules available in growing cells and the amount of cell wall substance formed, and they found that this ratio varied with the temperature. There are also many data concerning the difference in the auxin concentrations which promote or inhibit the growth of stems, buds, and roots (see THIMANN 1948). In other experiments THIMANN and SWEENEY (1937), SWEENEY and THIMANN (1938, 1942) and SWEENEY (1941, 1942) have shown that indole-3-acetic acid accelerates the protoplasmic streaming in epidermal cells of *Avena* coleoptiles as well as the elongation rate of these cells. In root hairs of *Avena* seedlings, too, the protoplasmic streaming was accelerated by indole-3-acetic acid, 10^{-4} to 10^{-5} mg per litre (*c.* 5×10^{-10} to 5×10^{-11} moles per litre) being the optimum concentration (SWEENEY 1944). LUNDEGÅRDH (1946), however, has shown that solutions containing 10^{-5} to 10^{-6} moles/litre indole-3-acetic acid do not immediately influence the elongation rate of root hairs of wheat seedlings. From my own experiments some preliminary results may be of interest to elucidate the different ways in which different cells or different parts of one cell can react to changes of the external conditions. The growth of intact wheat roots and their root hairs has been measured in the observation chamber in flowing *S*-solution with different amounts of indole-3-acetic acid. Arrangements were set up to make it possible to perform observations during 24–48 hours. During the whole experiments the solutions flowed through the chamber from a large container with the aired solution and in this way the concentration of the auxin in the medium was kept constant throughout the whole experiment. In other experiments the growth of roots and root hairs grown in culture tubes in the temperature control cabinet (see p. 9) was measured by the method described earlier (EKDAHL

1948 p. 129, plate II). The culture media were *S*-solutions with different amounts of 2,4-dichlorophenoxyacetic acid. The results show that indole-3-acetic solutions at first inhibited the growth of the roots almost completely (table 27), whereas the elongation rate of the root hairs was unaffected. The hairs elongated to lengths much higher (2 to 4 mm) than do hairs on roots grown in the ordinary *S*-solution. Rather rapidly, however, the roots adapted to the auxin solutions and after 24 hours they grew at an ordinary rate in solutions containing 0.5 to 1.0 μ *M* indole-3-acetic acid. In accordance with LUNDEGÅRDH's results (1946) these auxin concentrations were found to have no immediate effect on the elongation rate of the hairs when observed in the observation chamber. The 2,4-dichlorophenoxyacetic acid solutions also caused an inhibition of the root elongation and an increase in length of the full-grown root hairs. In these experiments, too, the roots adapted to the growth substance and after 48 hours' treatment the growth of the roots had begun to recover and the hairs grew to an ordinary length. The experiments will be continued and will be more exhaustively described and discussed in a later paper. Even at this stage, however, it may be pointed out that the observations are a good demonstration of the well-known fact that different cells can react differently to auxins and so can different parts of one cell. Unequal reactions of different cells or different parts of one cell may be due to differences in the composition of the protoplasm or the organization of the protoplasmic membranes (SINNOTT 1939; SINNOTT and BLOCH 1939 a, b; BLOCH 1943). Uniform or polar changes of the cytoplasm composition or the membrane organization may take place during the development of plant cells from the meristematic stage to the mature stage. When mature cells resume growth the protoplasmic membranes may be reorganized and some growth-regulating processes may be reactivated.

All the investigations mentioned and many others must be taken as a support of the opinion presented.

During the last fifty years many studies of the chemical composition of the root hair walls have been directed toward finding possible chemical differences between different portions of the wall and determining their bearing on the differences in physical properties existing between the wall of the extreme tip and the other parts of the hair wall. Such differences in properties have been found consistently by a variety of methods employed by numerous investigators (apical growth, plasmoptysis, distension of the apex: SCHWARZ 1883, HABERLANDT 1887 a, b, WORTMANN 1889, ZACHARIAS 1891, REINHARDT 1892, STIEHR 1903, HILL 1908, ROBERTS 1916, SCHAEDE 1923 a, b, SEIDEL 1924, JEFFS 1925, FARR 1928 d, HOLDHEIDE 1931, MCCOY 1932, CORMACK 1935, 1944, 1945, LUNDEGÅRDH 1946, EKDAHL 1948, KOPP

Table 27. Growth rate of wheat roots in nutrient solutions with indole-3-acetic acid.

Preliminary results from experiments with 2–3-day-old roots grown in the observation chamber in aired, flowing media at 20° C. See the text p. 51.

0–2 hours: *S*-solution.

2–27 hours: *S*-solution with different amounts of indole-3-acetic acids (IA) (concentrations given in μM per litre; 1.0 μM = 0.7 p.p.m.).

Time hours	Growth rate of roots in mm/hour				
	S-solution	*S*-solution + 0.5 μM IA	*S*-solution + 0.8 μM IA	*S*-solution + 1.0 μM IA	*S*-solution + 4.0 μM IA
1	0.8	1.0	0,9	1.0	1.0
2	1.0	1.0	1.0	1.0	0.9
3	1.1	0.3	0.2	0.2	0.2
4	1.0	0.2	0.2	0.2	0.1
5	1.1	0.2	0.2	0.2	0.1
6	1.1	0.3	0.2	0.4	0.1
7		0.4			
8	1.1	0.6	0.3	0.5	0.1
9					
10			0.4		
11		1.0		0.6	
12	1.1	1.0	0.8	0.9	0.4
23		1.2			
24	1.1		0.9		0.7
25		1.2	0.8	0.9	0.8
26	1.1	1.0		1.0	
27			1.0	1.0	

1948, and others). The results from microchemical tests, reviewed in detail by CORMACK (1949), however, are decidedly contradictory, which is perhaps partly attributable to actual differences in the plant materials studied. In addition, discrepancies may be due to differences in the analytic methods used. In spite of this it seems generally agreed that every portion of the cell walls of root hairs consists mainly of pectic and cellulosic substances, which in most cases are uniformly distributed in the hair wall and not separated into two distinct layers.

CORMACK has presented the most detailed and important hypothesis concerning the mechanism of growth of root hairs (1935, 1937, 1944, 1945, 1949). He assumes that the pectic substances (in this paper used in accordance with the definition given by KERTESZ 1951 a p. 6) in the hair wall determine the specific physical properties of the growing wall and limit the initiation and the growth of the hairs as well as their shape and size. In this process the calcification of pectic substances is thought to play an important role. CORMACK's hypothesis is based upon the following observations on growing root hairs or upon the results of microchemical tests of the hair wall composition.

"Root hairs are evaginations produced by internal pressure on plastic portions of an unequally hardened cell wall." (1935 p. 44.)

"The root-hair wall is composed of an inner layer of cellulose with an outer one of pectic substance . . . The pectic wall of the sides of the hair and of the epidermal cell on which a hair is growing is composed of calcium pectate. At the tip of the growing hair, it is sometimes composed of pectic acid and sometimes partly at least of calcium pectate. In the latter case, however, the wall covering the tip is soft and more delicate than that of the sides." (1935 p. 37.)

"Two conditions must be fulfilled if normal root hairs are to be produced. In the first place a supply of calcium in the form of a dissolved calcium salt must be present. Secondly, the hydrogen ion concentration must be such that the reaction between the calcium salt and the pectic acid of the cell wall may take place *gradually*. Through the gradual hardening of the cell wall vertical elongation is arrested and, due to increased pressure from within, the wall is pushed out at its softest point, invariably at or near the distal end of the cell." (1935 pp. 52–53.)

"When calcium is readily available, the softer more plastic area is confined to a narrow area at the tip, with the result that the growing hairs become long and straight and exceedingly narrow. On the other hand, where calcium is not readily available, the softer area becomes greatly extended with the result that the growing hairs become inflated, bulbous at the base and variously branched. Thus, the normal hair is always such as can be explained on the basis of internal pressure on a wall that has been gradually and equally hardened." (1949 p. 594.)

"Present evidence indicates that differences in plasticity are brought about by an increasing of calcification of the pectic layer from the tip of the hair to the base." (1949 p. 595.)

Through his investigations CORMACK has clearly shown that there are variations in the chemical composition of the pectic substances from different portions of the root hair wall. The microchemical tests used by CORMACK, however, do not permit the localization of gradual differences in calcification to different portions of the wall of the growing apex of the hairs, the elongating part having a length of 10 to 15 microns only (REINHARDT 1889; HABERLANDT 1887 a, b; see also p. 14). Further, CORMACK's results do not permit an estimation of how many carboxyl groups of the anhydrogalacturonic acid residues of the pectic substances are bound by Ca-ions or how many carboxyl groups are free or esterified (*cf.* BONNER 1936, 1946, 1951; KERTESZ 1951 a). According to HENGLEIN (1943, 1947; HENGLEIN *et al.* 1949), very small amounts of Ca-ions are sufficient for the formation of ionic bonds between polygalacturonide chains, and, further, the degree of esterified acid groups in the molecule chains strongly influences the possibilities of the pectic substances to bind the bivalent Ca-ions with one or two valencies. Pectic substances are highly hydrophilic colloids and their solubility, swelling capacity and other specific physical or chemical properties are easily changed through variations of the degree of esterification (see KERTESZ 1951 a; LINEWEAVER and JANSEN 1951). Therefore, the differences in calcification of the pectic substances of different portions of the hair wall are not the only possible cause of the strictly apical growth of the root hairs.

It is a great merit of CORMACK's work, however, that it has established the importance of pectic substances to the physical properties of the hair wall, especially in the softer, extreme tip area, and the fact that these substances play an important role in the growth mechanism of root hairs. CORMACK's supposition that the soft tip area is hardened from the very middle point of the curved area to the beginning of the cylindrical portion of the hair through a gradual calcification of the pectic substances in these portions of the hair wall cannot, however, be regarded as fully or definitely proved by the facts presented. Further, arguments against this hypothesis arise from some of FARR's as well as from my own results.

FARR (1927 a, b) found that root hairs of Georgia collards (a variety of *Brassica oleracea*) in solution cultures at pH 7.9 elongated at rates of about 50 μ/hour in 0.012 *M* $Ca(NO_3)_2$-solutions, at an average of 88 μ/hour in 0.008 *M* $CaCl_2$-solution, and at 66 μ/hour in 0.000010 *M* $Ca(OH)_2$-solutions. The proportions between the elongation rates in the three solutions, $Ca(NO_3)_2$:$CaCl_2$:$Ca(OH)_2$, were 100:176:132, but the concentrations of Ca-ions were in the proportions 100:67:0.08. Thus, in spite of the great differences in the concentration of Ca-ions in the culture solutions the growth rate of the root hairs varied relatively little, and FARR does not mention any differences in the shape of the hairs in the different solutions.

Further, if the concentration of $Ca(NO_3)_2$ was increased to 0.030 *M*, the growth of the hairs almost ceased at pH 7.9, but in a $CaCl_2$-solution with as high a concentration as 0.140 *M* FARR (1927 a p. 449, 1927 b p. 554) found a low but significant elongation of the hairs, the average rate being 10 μ/hour. These results are further established by FARR's repeated experiments (1928 a, b, c). Thus, the elongation rate of the hairs seems to be independent of the amount of Ca-ions of the external medium within a wide range of concentrations. This fact is supported by the results of LUNDEGÅRDH (1946).

In my own experiments the root hairs of wheat seedlings have been found to elongate at about the same rate in nutrient solutions with the concentration range 5 *S* to *S*/10 (exp. nos. 85–102). In other experiments the average length of full-grown root hairs in solutions diluted 25 times (exp. nos. 103–104) was only slightly less than the length in *S*-solutions. In solutions of pure $CaCl_2$ (0.001 *M*) the root hairs grew to only about 1:10 of the final length obtained in ordinary *S*-solutions, although the ratio between the Ca-ions in the two kinds of solutions was 1:1.5, and the relation between Ca-ions and Ca- + Mg-ions was 1:2.5 (exp. nos. 105–106). In all these experiments no differences could be detected in the mean diameter or shape of hairs in the different solutions.

The vigorous development of root hairs in moist air, where no external calcium supply is available, is another phenomenon that corroborates the fact that the initiation and the elongation of root hairs are not wholly dependent on the Ca-concentration in the external medium (table 28, plate II: fig. 8). It is of special interest to note that root hairs grown in moist air have about the ordinary size diameters, whereas roots grown in double-distilled water produce only very short hairs or hair-papillae.

It has been pointed out that a great many properties of the cells and the external conditions determine or influence the mechanism of the apical growth of root hairs and the growth in surface of the hair walls. It is impossible to determine in a single experiment what metabolic or biosynthetic processes are involved in the growth mechanism of the root hairs or to evaluate the degree to which internal or external factors influence or change individual component processes, and, consequently, the whole growth mechanism. In my investigations I have considered it most convenient to study as far as possible some properties and reactions of *growing root hairs only*. In chemical tests such as CORMACK's or in studying the structure of the hair walls under the electron microscope (FREY-WYSSLING and MÜHLETHALER 1949, 1950; *cf.* FREY-WYSSLING 1950 b; MÜHLETHALER 1949, 1950 a, b) it is very difficult — mostly impossible — to decide whether the object studied is a growing or a fullgrown hair. Furthermore, in such cases the question arises whether or not the properties or the structure of

Table 28. Maximum length and diameter of root hairs on roots from different plant species grown in nutrient solution and moist air.

Experiment no. 125.

Nutrient solution cultures: *S*-solution in culture tubes.

Moist air conditions: soaked seeds grown on moist filter paper in large Petri dishes at 20° C.

Cress = *Lepidium sativum*.

The values are means from 3–5 cultures.

Plant material	Nutrient solution			Moist air		
	Age days	Maximum length of root hairs μ	Diameter of root hairs μ	Age days	Maximum length of root hairs μ	Diameter of root hairs μ
Wheat	5	2 000–2 500	12–16	4–5	1 600–2 200	8–14
Oats	5	2 000–2 500	8–16	5–6	1 900–2 400	8–12
Rye	5	2 000–3 000	8–12	5–6	2 000–2 500	8–12
Corn	5	1 500–2 000	12–16	5	1 300–1 800	8–16
Radish	5	600– 800	12–16	4–6	2 900–5 100	8–16
Cress	5	1 500–2 000	8–16	4–5	2 200–3 100	8–12

the fresh hair walls have been changed during the preparation of the objects. If the mechanism of growth of hairs is to be studied, it seems most suitable to begin with the physiology of the root hair elongation and to determine the ways in which the elongation process can be modified by changes in the internal or the external conditions of the root hair cells.

The present part of my investigations furnishes some data concerning the consequences of changes of the turgor pressure with respect to root hair elongation, the elastic properties of different portions of the hair wall, and certain reactions of the root hairs to changes in the external conditions. Some other properties of the growing root hairs from the same plant material, grown under similar culture conditions, have been presented earlier by Lundegardh (1946), Kopp (1948) and Ekdahl (1948). With these data as a basis some conclusions and deductions as to the growth mechanism of root hairs can be made. Until further comparative data have been collected, their applicability must be restricted to the growth in surface of root hair walls only.

The growing root hairs of most plants are extremely narrow, cylindrical emergences. The growth in surface of the hair wall is restricted to a very small apical portion, which also has a much higher extensibility than the wall of the longer basal part. The longitudinal extensibility of the mature wall of the hair cylinder is found to be very low (table 2), whereas the

turgor pressure extends the hair wall in the transverse direction by about 5 per cent. A cell wall composed mostly of cellulosic and pectic substances and with the above properties, may be expected to have the main part of the cellulose in crystalline fibrils, which are preferably oriented in the direction of the long axis of the hair, and with pectic substances as an incrusting cement. The cellulose fibrils are not very tensible, but the amorphous pectic substances between the cellulose microfibrils and fibrils in the wall are highly hydrophilic and easily tensible, and thus permit a transverse extension of the hair wall.

These conclusions are in very good agreement with the observations of Frey-Wyssling and Mühlethaler (1949, 1950) on root hairs of onion seedlings. From observations with the polarizing microscope and electron micrographs of hair walls they have proved that the mature hair wall consists of a loosely textured cellulose network with the cellulosic microfibrils partly scattered but preferentially oriented in the direction of the long axis of the hair cylinder. This is shown strikingly in the excellent electron micrographs prepared by Mühlethaler (Frey-Wyssling and Mühlethaler 1949, 1950).

Thus, the physical properties of the mature hair walls seem to depend on the cellulosic as well as on the pectic components which determine the micromorphological structure of the wall.

The wall of the growing apex of the hair has properties quite different from those of the mature wall of the cylindrical portion of the hair or of the thickened apical wall of a mature non-growing hair. The former is characterized primarily by its capacity to enlarge, but its chemical and physical properties are also distinctive. Cormack (1935, p. 37) found that the cellulose in the walls of growing root hairs was more easily hydrolyzed than the cellulose in the walls of mature hairs. Furthermore, staining with some cellulose reagents does not give the same result for growing apical walls as for mature wall portions. This latter fact has been observed by Kopp (1948, p. 300) as well as by myself, and the observed behaviours of the apical wall are rather similar to those found in primary walls of meristematic cells (Tupper-Carey and Priestley 1923; Anderson and Kerr 1938; Frey-Wyssling and Mühlethaler 1949; Flint 1950; Frey-Wyssling 1952 a), so that, in fact, the apical wall of elongating hairs can be characterized as a primary cell wall in the growing stage.

Thus, it may be pertinent to summarize briefly what we know about the structure and the properties of elongating primary cell walls, although it must be presumed that the mechanism of the apical growth of root hairs may be unique in certain details.

From the results of X-ray and polarizing microscope studies of cell walls

of higher plants FREY-WYSSLING (1948 a) has further developed NÄGELI's micellar theory. According to FREY-WYSSLING, the cell wall consists of long strings of cellulose crystallites which are supposed to form a submicroscopic network. This cellulose framework gets a certain rigidity through coherent "junctions" (1948 a p. 47), cohesion at the points, where the microfibrils are in contact with each other. FREY-WYSSLING (1948 a p. 175) assumes that even quite young meristematic cell walls contain a submicroscopic cellulose framework. The elongation of the meristematic or the young cell walls, *i.e.* the growth in surface of the primary cell walls, is brought about by a loosening of the "junction points" in such a way that the chain molecules of the crystal lattices separate by parallel displacement.

> "The area then becomes larger because spaces are formed which are free from cellulose. The loosened structure may become more dense again as fresh cellulose chains are woven in between the separated strands. This process constitutes intussusception." (FREY-WYSSLING 1948 a, p. 177.)

Thus, the capacity for growth in surface, extensibility and other properties of primary cell walls, as understood by FREY-WYSSLING, are influenced primarily by properties of the crystalline cellulose framework of the wall. However, FREY-WYSSLING's opinion has changed gradually during the last few years to comprise the supposition that, in some cases, the growth in surface of primary cell walls is localized to small portions of the wall surface (1949 p. 79, 1950 b, 1952 a, b), and that the elongation in some way involves a loosening of the cellulose network through dissolution of some few cellulose strands.

HESS and collaborators (HESS 1943 a, b; HESS *et al.* 1936; HESS *et al.* 1939; HESS *et al.* 1942; WERGIN 1940, 1942) assume that pectic substances are the continuous phase in native primary cell walls and that the cellulose is in a non-crystalline stage. The main part of the chain molecules of cellulose, however, are thought to have a parallel orientation. Not until the non-cellulosic substances, mostly pectic substances, had been removed, could HESS *et al.* demonstrate any cellulose crystal lattice in the primary cell wall by means of the X-ray method. SISSON (1936, 1943) has made similar observations. HESS and his coworkers conclude that the properties of native cellulose fibres are not derived from the chemical and the physical properties of the cellulose chain molecules, but principally from the physical and chemical inhomogeneity of the cell wall.

From X-ray diagrams and electron micrographs PRESTON and co-workers (PRESTON *et al.* 1948 a, b, 1950; PRESTON and WARDROP 1949) have deduced that even fresh or wet cell walls contain crystalline cellulose, and PRESTON (1952 a p. 176) emphasizes that "the absence of an X-ray diagram does

not at all imply that there are *no* crystalline regions but merely that those which do occur are too small in width (estimated to be somewhat less than 20 Å.) to give a crystalline pattern". PRESTON *et al.*, however, have not been able to state definitely that primary cell walls have an organized crystalline cellulose network, but PRESTON (1952 a, b; PRESTON *et al.* 1950) has pointed out the importance of the ratio between crystalline and non-crystalline fractions in cell walls to the properties of the walls. From these observations PRESTON (1952 a p. 178, fig. 60) deduces that primary cell walls have a cellulose structure with fibrils running in a direction preferably transverse to the longitudinal cell axis.

Recently, KERR (1951) discussed the growth and structure of primary cell walls and concluded that it is highly improbable that the cellulose chains in fresh primary walls form a crystalline network. He also points out that a fibrillar network of cellulose crystallites will not have the elastic extensibility of primary cell walls. KERR bases his conclusion on the facts that the cellulose of primary walls shows the properties of a skeletal network only after drying, stretching or other preparatory treatments (*cf.* ANDERSON and KERR 1938; BERKLEY 1939, 1942; BERKLEY and KERR 1946).

Furthermore, KERR emphasizes that the structure and properties of pectic substances most probably are of considerable importance in determining the nature of the primary wall and the mechanism of its growth. KERR concludes with the following hypothesis (1951, p. 42):

"Considering all the properties of pectic substances, the property of the primary wall could be explained if it were assumed that the pectic substances were the continuous phase of the wall and the cellulose microfibrils were a discontinuous phase of the wall. The cellulose fibrils might be considered as structural reinforcement. Changes that occur during growth would affect the easily hydrolyzable pectic substances and not the cellulose. Changes in elastic extension of the wall could be explained as changes in hydration of the pectic gel. This hypothesis has not been proved but it has been brought forward to get around the impasse that the properties of the primary membrane are not the properties of a sheet of cellulose."

On the basis of observations of the elastic properties of higher plant tissues, TREITEL postulates that "the submicroscopic structure of secondary cell walls, of plant tissues of higher plants is composed of partly crystalline and partly amorphous cellulose" (1946, p. 368). Further, TREITEL assumes that primary cell walls have only amorphous cellulose in their submicroscopic structure.

"The submicroscopic structure of the highly plastic primary cell wall is given by a molecular network of cellulose. In this network there is no cross-linking, the chain molecules of cellulose are only entangled with each other. The physical part of growth of primary cell walls is explained by passages of glucose units from protoplasm to

the meshes of the cellulose network in the primary wall. The plasticity of this wall is great because the meshes contain fat and wax and because the loose molecular chains of cellulose are easily moved. The pressure of turgor producing the motion of glucose to the primary wall must be greater than the yield value for this wall. In this case a plastic deformation of the wall is possible." (1946, p. 368.)

Thus, TREITEL, as well as KERR, assumes that there are no cross-linkages or any specific bindings between the cellulose chain molecules in the growing primary cell walls.

In all investigations referred to and in many others concerning the mechanism of growth in surface of cell walls the main problem has been to observe the chemical composition or the physical structure of the walls and, in particular, to determine whether or not the cellulose is in a crystalline state. Several investigators deny the existence of crystalline cellulose in fresh, elongating cell walls and maintain that the crystal lattices are formed in connection with stresses on the cell wall or after changes of the material during its preparation for observations. Others, however, have found crystalline cellulose even in untreated, fresh cell walls. It can be stated, however, that no definite data are available concerning a direct observation of crystalline structural cellulose in any *fresh and growing cell wall*, neither in the meristematic nor in the elongating state. For further details reference is made to TREIBER's (1951 a, b) review of the structure and properties of both primary and secondary cell walls and to the surveys of FARR (1944) and PRESTON (1952 a, b).

In my investigations I have as yet made no direct analysis of the micromorphological structure or detailed composition of the fresh growing hair walls. An attempt, however, will be made to evaluate the extent to which the reactions of root hairs and the properties of their walls, as revealed in the present study, can be made to fit in with the different hypotheses concerning the growth in surface of primary cell walls, and thus to deduce how far any of these hypotheses may be applied to the growth of root hairs. The following four properties of the hairs and their apical walls have been found particularly characteristic, and they also seem to be of special significance for the interpretation of the growth mechanism of root hairs:

a. the extensibility of the apical hair wall
b. the high turgor pressure of the hairs
c. the resumed growth from more or less globularly extended hair tips with thickened walls
d. the plasmoptysis, which can be caused in several different ways.

Furthermore, the apical hair walls are supposed to consist mainly of pectic substances, but also to involve cellulosic constituents, which is

evident from earlier investigations surveyed and discussed by Cormack (1949).

The apices of growing root hairs have a conical shape and probably have their highest extensibility at the very tip. Toward the base of the apex the wall is more rigid and at the beginning of the cylindrical portion of the hair the wall is almost mature (Reinhardt 1892, 1899; Lundegårdh 1946; *cf.* p. 13). It may be presumed that the root hairs owe their very narrow tubular shape to the fact that their high turgor pressure extends the extreme apical portion of the growing hair wall more than the other portions, and that the differences in the extensibility of the different portions within the hair apex are maintained during the whole growth period. If the elongation of the hairs is checked, *e.g.* through mechanical disturbances, the properties of the apical wall will be immediately changed. This part of the hair wall has still a higher extensibility than the mature side walls but the gradient of the softness within the apical wall portions has disappeared so that every portion of the apical wall will be extended to about the same degree. It may be assumed that the processes, which continuously weaken the very middle point of the apical hair wall, are immediately checked or changed but that, in most cases, it takes some time before the wall is hardened. The result is that the turgor pressure causes the apex to expand into a more or less spherical form (see fig. 1 p. 25; plate I: fig. 3 and plate II: fig. 11).

These spherical protuberances of the hair apices are of rather variable size. Sometimes, the variations can be rather great, and some few apices do not swell up at all. Soon after the apical wall has begun to bulge, it is also found to be thickened. It seems very probable that the rate of the thickening process is a most important factor determining the final size of the swellings. A rapid thickening of the wall will result in a rather small extended hair sphere, and a slow apposition of wall particles gives a highly extended hair apex. Sometimes, however, no thickening of the wall will be seen in the cases of failure of extension, but instead wall substances are formed inside the wall and are precipitated in more or less irregularly formed portions at the very middle point of the hair apex (plate I: fig. 7). In these cases the apical wall has stiffened immediately and the formation of new wall substances has been restricted to that point of the hair apex where the growth in surface of a normal hair is highest. A similar phenomenon has been observed by Wortmann (1889), Reinhardt (1892), Zacharias (1891), Windel (1916), Hopmann (1930), and Lundegårdh (1946). Gorter has found a much more extensive formation of cell wall substances on the inside of the root hair apices of *Hyacinthus* after treatment with colchicine (1945) and inside the tips of *Lepidium* hairs as a result of growth failure after treatments with triiodo-benzoic acid (1949 a, b). Boysen Jensen

(1950), too, observed intensive production of wall material inside the walls of root hair tips of *Lepidium* and *Phleum* after growth stoppage. The fact that wall substances can be formed and laid down in the absence of elongation of the hairs is also shown in weakly plasmolyzed hairs, in which a new wall is formed on the surface of the naked apex of the retracted protoplast (see p. 21; plate I: fig. 2). In this case the protoplasm has kept its ordinary active streaming and no changes in the appearance of the protoplasm have been observed. Thus, the outer protoplasmic membrane has been loosened from the hair wall without losing its capacity to form wall substances; but if the turgor pressure is re-established, there will be no stretching of the new wall which may, in fact, burst occasionally.

Boysen Jensen (1950) presumes that the wall material formed inside the tip wall mainly consists of cellulose, and with the help of electron micrographs Frey-Wyssling and Mühlethaler (1949, 1950) have shown the presence of cellulose microfibrils in mature portions of onion root hairs. In no case, however, has it been possible to show that the growing apical walls of root hairs are built up by an organized network of cellulose microfibrils, but it seems to be obvious that the apices of the hairs consist mainly of amorphous pectic as well as of cellulosic substances, and it seems rather probable that the pectic substances form the main constituents. As has been pointed out earlier (p. 55), the author does not believe in Cormack's hypothesis which states that the apical hair wall is hardened by formation of calcium pectates, but I consider it most likely — as a working hypothesis — that the apical hair walls are loosened by pectic enzymes and matured by a crystallization of amorphous cellulosic substances and the formation of microfibrils in the apical walls. The crystallization of cellulose and the formation of cellulose strands may be brought about by the stretching of the growing wall in a similar way as Berkley and Kerr (1946) found for fresh primary walls of young cotton fibres.

If hairs with such spherically extended and thickened apices are left undisturbed in a suitable medium for some time, some hairs begin to grow again. The first indication of a resumption of growth is the loosening and thinning out of the thickened wall in a small area of the spherical apex (plate I: fig. 4). This behaviour may be observed in a flowing medium of constant chemical composition and without any changes in other experimental conditions. Thus, it must be an endogenous process which exerts its effect in a polar manner. Very probably the same protoplasmic systems are involved in softening the localized areas of the walls of young epidermal cells, from which the young root hair papilla grows out, and some of these systems may continue to operate in the extreme apical portion of the hairs (*cf.* Bloch 1943; Sinnott 1939; Sinnott and Bloch 1939 a, b). The

resumption of growth in a thickened, spherically extended hair apex as well as the precipitation of wall substances at the extreme apical point of the hair may indicate that enzyme systems which can decompose as well as synthesize pectic and cellulosic substances, are polarly localized to the very hair tips. These facts may be taken as a support of my hypothesis which states the importance of pectic enzymes to the gradually loosened apical hair wall and thereby constitutes a factor primarily regulating the elongation of root hairs.

This hypothesis is further supported by the results of the experiments on the effects of changes in turgor pressure on the elongation rate of the hairs. It has been shown that the hairs have a high turgor pressure, but, in addition, the results from my experiments show that the elongation rate of the hairs is not, or only slightly, influenced by moderate variations in the turgor pressure. Thus, it can be stated that the high turgor pressure provides the force necessary for the elongation of the apical hair wall, but in most cases it is greater than required and is therefore no rate-regulating factor in the elongation of the hairs.

The elasticity of the apical hair wall is found to be entirely in accordance with KERR's (1951) characterization of primary cell walls. During the spherical extension of the hair apex its wall reacts rather as if it were built up by a substance with rubber-like properties than by a substance with the properties of a cellulose sheet. This seems to agree rather well with FREY-WYSSLING's idea about the composition and the micromorphological texture of primary cell walls (FREY-WYSSLING 1949, 1950 a, 1952 a pp. 322–323). With the help of electron micrographs FREY-WYSSLING and collaborators (FREY-WYSSLING *et al.* 1948; FREY-WYSSLING and MÜHLETHALER 1949, 1950; FREY-WYSSLING and STECHER 1951; MÜHLETHALER 1950 a; STECHER 1952) have shown that young cell walls are constituted by a loosely textured cellulose framework with the microfibrils highly scattered and interwoven. The spaces in the cellulose network are incrusted by cytoplasm, or by other cell wall constituents, in most cases highly hydrated pectic substances and hemicelluloses. It is assumed that the growth in surface of primary cell walls is localized to small portions of the wall surface ("mosaic growth"), and that the elongation in some way involves a loosening of the cellulose framework through dissolution of some few cellulose strands, extension of the loosened wall portions and a repeated hardening by intercalation (intussusception) of new microfibrils (FREY-WYSSLING 1949 p. 79, 1950 a, 1952 a, b; FREY-WYSSLING and STECHER 1951; STECHER 1952). FREY-WYSSLING (1952 a) emphasizes that there will be some handicap in the electron microscopy as the objects must be studied completely dried and in vacuum. With respect to the identification of microfibrils in primary cell walls by electron

micrographs FREY-WYSSLING remarks: "Only when this highly hydrated, spacious network is freed from non-cellulosic substances and completely dried does it furnish the picture of a dense interwoven texture in the electron microscope" (1952 a p. 322).

In spite of modern methods and intensive and exhaustive investigations, our knowledge about the growth in surface of primary cell walls is rather vague. The results available seem to be too incomplete to give full support to the presumption that cellulose microfibrils in primary cell walls are joined to a more or less rigid framework. It may be equally possible that the growing areas mainly consist of pectic substances (KERR 1951) and that the cellulose in primary cell walls forms a network of molecule chains without any cross-linkages (TREITEL 1947). Intercalation (intussusception) of new wall substances does not presuppose an immediate formation of new cellulose strands in the walls. Concerning the elongation of root hairs it seems rather possible that the growing apical walls mainly consist of pectic substances and that the continuous softening of the apical wall takes place through the action of enzymic processes in which preferably pectic enzymes are involved. The hardening of the wall from the very tip to the sides may — according to the author's opinion — take place through a gradual formation of cellulose strands, which are first dispersed, but, as the wall is thickened and matured, will be oriented in the direction of the long axis of the hairs (*cf.* FREY-WYSSLING and MÜHLETHALER 1949 and p. 58).

The supposition that pectic enzymes are present and functioning in the growing hair apex seems to be supported by the observations on plasmoptysis of root hairs in solutions of sodium chloride or calcium chloride. As mentioned earlier (see p. 55), the properties of pectic substances are highly dependent on the degree of polymerization of the polygalacturonide molecule chains and on the number of free carboxyl groups per unit chain length. Of special interest is the formation of calcium pectates, particularly because bivalent Ca-ions may combine with two carboxyl groups, one from each of two molecule chains. In this manner two or more molecule chains can be linked together into a molecular network (HENGLEIN 1943, 1947, 1949; LUNDEGÅRDH 1946). Such linkages are formed already in the presence of small quantities of Ca-ions (HENGLEIN 1943, 1947; HENGLEIN *et al.* 1949), but the possibilities for the formation of ionic bridges between the molecule chains depend, to a great extent, on the degree of esterification of the pectic substances (KERTESZ 1951 a, b). The course of esterification or deesterification of pectic substances must therefore play an important role in the formation of a cell wall if its physical properties are determined primarily by its pectic components.

The nature of the enzyme systems active in the final formation of cellulose

or pectic substances in cell walls is quite unknown. The results from the enzymic decomposition of pectic substances, however, may permit some conclusions as to the enzymes regulating the latter processes. There are two pectic enzymes which are of special interest, namely, pectinesterase and polygalacturonase (for definitions see LINEWEAVER and JANSEN 1951). The pectinesterase (PE) "catalyses the hydrolysis of the ester bonds of pectic substances to yield methanol and pectic or pectinic acids." Polygalacturonase (PG) "catalyses the hydrolysis of glycosidic bonds between de-esterified galacturonide residues in pectic substances" (*l.c.* p. 269). The author fully realizes the difficulties of making generalizations from results of specialized investigations as well as the differences between the chemical pathways of decomposing and synthetic processes (see BALDWIN 1952), but nevertheless I consider that some results as to the regulations of the action of these enzymes may be of interest in order to elucidate the presented hypothesis concerning the growth mechanism of root hairs. JANSEN and MACDONNELL (1945) have found that the ratio between the degree of esterification of pectic substances and the activity of PG changes inversely with changes in the methoxyl content of the pectic substrate. It may be supposed that the course and the degree of esterification of pectic substances with short molecule chains influence their transformation into the long macromolecules forming the pectic constituents of the cell wall. Furthermore, several investigators have shown that cations may greatly affect the activity of PE (LINEWEAVER and BALLOU 1945; JANSEN, MACDONNELL, and JANG 1945; MACDONNELL, JANSEN, and LINEWEAVER 1945; MCCOLLOCH and KERTESZ 1947; see also LINEWEAVER and JANSEN 1951, and KERTESZ 1951 a, b), but the cation effect on PG of higher plant origin, though little known, seems to be rather slow (see KERTESZ 1951 b pp. 759–760; LINEWEAVER and JANSEN 1951 p. 787). Thus, LINEWEAVER and BALLOU (1945) have shown that low concentrations (up to 0.02 *M*) of calcium salts had a strongly stimulating effect on the action of alfalfa PE and that sodium salts in the same concentration range had a lower but appreciable effect. In higher concentrations the effect of Ca-ions was considerably smaller and fell rapidly with increased concentration, whereas the effect of Na-ions continued to rise to the maximum value obtained with Ca-ions, and remained at this value over a wide concentration range (0.10–0.20 *M*).

About the influences of sodium and calcium ions on the activity of PG there are only a few data available (see KERTESZ and MCCOLLOCH 1950; KERTESZ 1951 b; LINEWEAVER and JANSEN 1951), but MATUS (1948) has shown that cations can increase the PG-activity and that the activation is increased with the valence of the cation. As far as we know, sodium and calcium ions have no considerably stimulating effect on the activity of cellu-

lose enzymes (see PIGMAN 1951; SIU 1951). FAHRÆUS (1947) as well as NORKRANS (1950) found that calcium ions had no effect on the activity of cellulose decomposing enzymes.

As found already by STIEHR (1903), and confirmed by the author, root hairs are plasmoptyzed in sodium salt solutions as well as in solutions of calcium salts. In pure sodium salt solutions the root hairs burst within the concentration range 0.03–0.14 *M*. Addition of calcium to these solutions decreases the intensity of the plasmoptysis (tables 21–23). But in pure calcium salt solutions root hairs burst within the concentration range of 0.01–0.08 *M*. Since the addition of calcium ions to the sodium salt solutions decreases the plasmoptysis, *i.e.* hardens the apical hair wall, the author found it necessary to reinvestigate the effects of pure calcium salt solutions. The experiments were repeated many times and at different dates with consistent results: the root hairs often burst in calcium salt solutions. There is, however, an important difference between the course of the plasmoptysis in sodium salt solutions and that in calcium salt solutions (p. 43, table 23). In the first case short as well as long hairs burst, but in calcium salt solutions very short hairs (< 50 microns) are only plasmoptyzed. If we assume that the physical properties of the growing hair wall are determined primarily by the pectic substances of the wall and that the growth of the wall is regulated by pectic enzymes, the difference between plasmoptysis in sodium and in calcium salt solutions may be explained by the results of LINEWEAVER and BALLOU (1945) concerning the effects of sodium and calcium ions on the activity of pectinesterase (PE), and the low effect of these ions on the activity of polygalacturonase (PG) (see KERTESZ 1951 a, b; LINEWEAVER and JANSEN 1951). In root hair papillae and short hairs which have not yet reached the ordinary optimal elongation rate, the enzymes bring about a partial loosening up of the cell wall in local areas, which were already partly hardened. This loosening must involve a dissolution of strands of crystallized cellulose. In long hairs, which have a very uniform elongation rate, however, the enzyme system must cause a uniform growth in surface of the apical hair wall and also regulate the hardening of the wall from the extreme apical point towards the beginning of the cylindrical portion of the hair. Thus, the organization of the enzyme systems influencing the wall of long hairs may be somewhat different from that of short hairs, and the reaction to calcium ions may not be the same.

However, our knowledge of the occurrence and the activity of pectic and cellulosic enzymes in higher plant cells is too meagre to permit concrete conclusions as to the importance enzyme processes have for the growth mechanism of root hairs and primary cell walls. The foregoing discussion has been made to indicate the importance of enzyme reactions to the growth

of cell walls and to establish that pectic substances very probably are highly determinative to the growth of the apical wall of root hairs. Team works including studies on the composition and texture of fresh primary cell walls and the enzyme reactions active in the formation of cell wall constituents and in their intercalation in the elongating cell wall of higher plants, combined with observations of different physiological processes, will be necessary for a future understanding of the mechanism of the growth in surface of primary cell walls.

It is often rather difficult to apply results from laboratory experiments to field conditions. Two of the conditions of root hairs found in my investigation, however, are so obvious that they must be considered determinative of the reactions of root hairs under field conditions, too. These two conditions are (1) the very low extension of the hairs in the direction of the long axis, and (2) their high ability to adapt to changes in the osmotic pressure of the external medium. Both these conditions must play an important role in the function of root hairs in the field, especially under extreme conditions, when the soil rapidly changes its humidity or its osmotic conditions.

One of the functions of root hairs is to fasten the plants to the soil. For this function the low extension of the hairs must be of great importance as the risk for the hairs to be contracted and torn off will be rather small.

The most important function of the root hairs is to increase the contact between the root surfaces and the soil particles and to participate in the absorption of water and inorganic salts. For these vital functions it must be highly essential that the root hairs are not put out of function by sudden changes in the osmotic pressure of the soil water.

Summary.

The results presented in this paper form part of my studies of the growth and the function of root hairs. In the experiments presented special interest has been devoted to the osmotic conditions of growing root hairs and to studies of the effects of changes of these conditions and the consequences of these changes for the growth and the elongation rate of the hairs. The results are compared with previous experiments concerning root hairs carried out at the Institute by Lundegårdh (1946), Kopp (1948) and Ekdahl (1948). Finally, the mechanism of root hair elongation has been discussed.

1. Root hairs are cylindrical emergences growing out from the root epidermal cells. To distinguish between the hair-forming cell proper and the hair protruding from this cell, the two parts are referred to as *hair-cell* and *hair*.

2. Most of the observations were made on hair-cells and hairs of *roots of intact seedlings* of spring wheat grown in nutrient solution under artificial illumination. Grown in water or in weak nutrient solution of the standard composition (*S*-solution, p. 9), the hairs are completely turgid and in this *S*-solution they reach lengths of 1 to 2 mm, but their diameters are 10 to 15 microns only. The elongation rate and some of the reactions of the root hairs have been studied on hairs grown in flowing media in an observation chamber placed on the stage of a microscope. The main progress of the experimental procedure has been earlier described in detail (Lundegårdh 1946; Ekdahl 1948), but some modified arrangements are mentioned. The mean elongation rate of the hairs was found very constant and in the *S*-solution it has been about 90 μ/hour (p. 32; Ekdahl 1948, p. 119).

3. Some concepts of osmotic quantities have been defined. The terms used have been chosen for being best suited to explain the osmotic conditions of plant cells.

4. The turgor extension of mature hair-cells was found to be very low, about 1.5 per cent. Growing hair-cells at a distance of 5 mm from the root tips were extended by the turgor pressure to about 11 per cent (table 1). The volume of mature hair-cells at the incipient plasmolysis stage has been calculated to be about 4.5 per cent lower than the initial volume (p. 11).

5. A method is described with which intact root hairs can be plasmolyzed in such a way that the protoplast is loosened from the cell wall at the very hair tip only, and without any loosening of the protoplast from the cell wall in the hair-cell. As plasmolysis proceeds, the protoplast contracts downward in the hair until an equilibrium stage is reached (plate I: fig. 1). The naked apical surface of the protoplast in a plasmolyzed hair retains its capacity to form wall substances (p. 21; plate I: fig. 2). With this method the earliest stage of incipient plasmolysis in the hair apex is easily noticeable.

6. The turgor extension of the cell walls in the longitudinal direction of the hairs proved to vary with the length of the hairs. For root hairs less than 100 microns in length it is about 3 per cent, but for longer hairs it was found to be very low, or less than 1 per cent (table 2). This fact has been found to be similar in root hairs from three other plant species (table 3).

7. It is found that the root hairs elongate in their apices only and that the zone stretched by the turgor pressure is not longer than 10 to 15 microns (p. 14). If the turgor extension of the wall in the longitudinal direction is referred to the stretching zone only, it has been calculated to be 5 to 10 per cent or of the same magnitude as for root epidermal cells during their elongation period (table 1, and Burström 1942 a).

8. The turgor extension of the wall in the transverse direction of the hairs is uniform along the whole length of the hairs and was found to be 4 to 5 per cent. The results have been obtained after measurements from two different methods: plasmolysis and plasmoptysis caused either by *S*-solution poor in oxygen or by sodium chloride solutions (tables 4–6).

9. The volume of growing root hairs at the incipient plasmolysis stage has been found to be 8 to 10 per cent lower than the initial volume (p. 18). For longer hairs ($> 100\,\mu$) this decrease in volume is independent of the hair length. The volume of the whole hair-forming cell, *i.e.* hair-cell + hair, varies, however, with the length of the hairs, but the variation is not very high (table 7).

10. Root hairs of wheat seedlings grown in weak nutrient solution are found to have a high osmotic pressure and a high turgor pressure, the latter having been calculated to be 6.8 to 7.8 atm. at the fully turgid stage of the cells and measured at 20° C (table 8). No differences between the turgor pressures of hairs of different lengths ($> 100\mu$) have been found. The osmotic pressure of the hairs proved to increase almost in direct proportion to increases of the osmotic pressure of the culture medium.

11. It was found that the apical walls of growing root hairs have a high rigidity. If the turgor pressure of the hairs is increased, the hairs burst in their tips (plasmoptysis), but the apical hair walls can withstand an in-

crease in turgor pressure of about 3 to 4 atm. before the hairs burst (p. 24, table 9). When the hairs do not burst, their tips become more or less distended (fig. 1; plate I: fig. 3; plate II: fig. 11). Such distensions of the very hair tips are ordinary consequences of sudden disturbances of the hair growth.

12. The growth and the elongation rate of root hairs after a lowering of the osmotic pressures of the media, *i.e.* after increases of the turgor pressure, have been studied (tables 10–15). Experiments were carried out in two series. In the first series the roots were grown in media with different osmotic pressures obtained by addition of different amounts of NaCl to the *S*-solution ($S + 1.0 - 3.0$ atm. NaCl) and the media were then changed to *S*-solution. In the second series the roots were grown in nutrient solutions of different concentrations (10 *S* to *S*) and the media were changed to solutions of lower concentrations (*S* to *S*/10). In both series the root hairs elongated at an ordinary rate before the change of medium. After moderate increases of the turgor pressure of the hairs caused by the changes of media, the hairs either continue to elongate without any interruption, but at a more or less lowered rate, or they completely stop growing for some time. The tips of hairs with ceased elongation at first become more or less distended but rather soon most of them resume growth (plate I: figs. 4–5). High increases of the turgor pressure caused plasmoptysis of the hairs.

13. It is shown that high increases of the turgor pressure cause the hairs to burst, but plasmoptysis also occurs in strong salt solutions, *i.e.* after lowering the turgor pressure. Thus, root hairs grown in *S*-solutions were found to burst after transference into NaCl-solutions, KCl-solutions, $CaCl_2$-solutions and glucose solutions (tables 19–25). Plasmoptysis was most frequent in 0.05–0.12 *M* NaCl-solutions. Calcium ions proved to decrease or inhibit the plasmoptysis in sodium chloride solutions. Contrary to that, root hairs burst in pure calcium chloride solutions, but there has been found a difference between the plasmoptysis in the sodium solutions and that in the calcium salt solutions. Sodium ions cause plasmoptysis of most elongating root hairs, while the Ca-solutions cause a bursting of the apical wall of very short hairs only ($< 50\ \mu$). The bursting of the hairs can be weak and the hairs may recover their ordinary protoplasmic streaming and some of them resume growth (plate I: fig. 6; and plate II: fig. 9). In other hairs the plasmoptysis is strong and the protoplasm coagulates and dies (plate II: fig. 10). The elongation rate of root hairs was determined after changes of the medium from *S*-solution to $S + 2.0 - 3.0$ atm. NaCl-solutions. The changes caused only a temporary lowering of the elongation rate of some hairs but caused an immediate stoppage of the growth and a distension of the apical portions of some other hairs. In most cases, ceased elongation is followed by a rapid resumption of growth. Some distended hairs, however,

form very thickened apical hair walls and do not elongate any more. Other hairs are plasmoptyzed.

14. The results from the experiments in which the turgor pressure of the root hairs is changed, increased or decreased, have given good evidence to the great ability of the hairs to overcome differences in the osmotic pressure of the surrounding medium. Further, the reaction of the hairs to changes of the turgor pressure was the same whether the turgor pressure was increased or decreased.

15. Some preliminary experiments have been mentioned which show that concentrations of indole-3-acetic acid inhibiting the growth of the roots have no immediate effect on the elongation rate of root hairs. In flowing *S*-solution with indole-3-acetic acid — 0.5 to 1.0 μMol per litre — the elongation of the roots is at first completely stopped, but after 24 hours the elongation rates are more or less recovered (table 27).

16. In the discussion the reactions and the properties of the apical wall of growing root hairs have been compared with different hypotheses concerning the growth in surface of primary cell walls. It has been emphasized that the properties and the compositions of apical walls of growing root hairs are mostly in accordance with the postulates concerning primary cell walls made by Kerr (1951) and Treitel (1947). The pectic constituents of the apical hair walls are considered to be of great importance to the growth mechanism.

17. The elongation rate of root hairs seems to be almost independent of the concentration of calcium ions in the external medium within a wide range of concentrations, as found by the measurements of Farr (1927 a, b), Lundegårdh (1946) and from my own experiments. For this and other reasons the author cannot believe in Cormack's hypothesis concerning the growth of root hairs. Cormack states (1935, 1949) that the shape and the elongation of root hairs are highly dependent on the concentration of the calcium ions of the surrounding medium and that the hardening of the apical hair walls takes place through a gradual formation of calcium pectates. It is, however, a well-established fact that root hairs develop very well in moist air.

18. The author presents the following hypothesis, which is not fully proved but must be taken as a working hypothesis. It is based on the supposition that pectic substances are highly important to the elongation of root hairs and that pectic and cellulosic enzymes, especially the pectic ones, may be responsible for the continuous loosening of the extreme apical portion of the hair wall. The pectic and the cellulosic constituents in the growing apical hair wall are probably amorphous and highly hydrated, and the wall may be hardened by crystallization of cellulose and formation of cellulose

strands. This may take place gradually from the extreme apical point to the cylindrical portion of the hair. The cellulose microfibrils are at first dispersed, but as the wall matures the orientation of the strands is more or less parallel, mainly in the direction of the long axis of the hairs (p 65).

19. It is often difficult to apply results from laboratory experiments to field conditions. However, the extreme rigidity of the hair walls in the longitudinal direction of the hairs, and the capability of root hairs to adapt to changes in the osmotic conditions of the external medium, must be of great importance to the function of the hairs also under field conditions.

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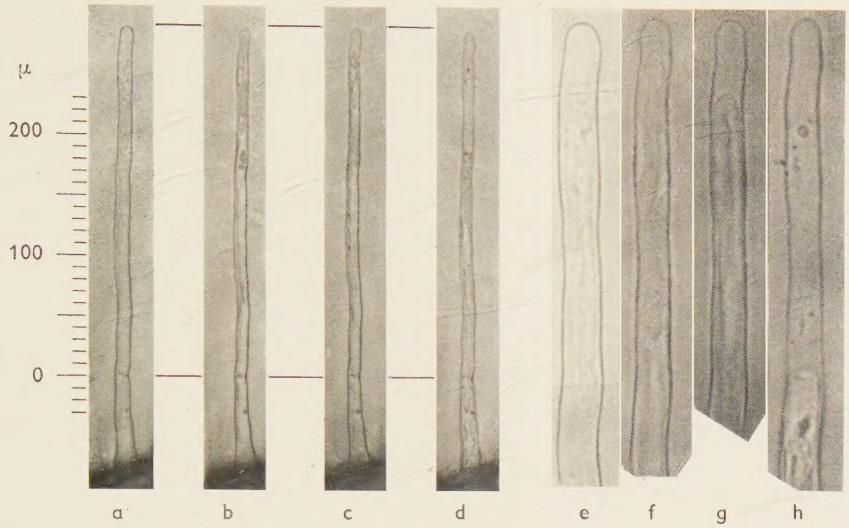

Fig. 1. The course of tip plasmolysis of a root hair from a wheat seedling. See the text p. 12. Magnification: **a**—**d** *c.* 160 ×; **e**—**f** *c.* 400 ×. **a** and **e**: 0 min. = just before the change of medium. **b** and **f**: 30 min. = 10 min. in plasmolytic medium *S* + 9.0 atm. NaCl and 20 min. in *S* + 11.2 atm. NaCl. **c** and **g**: 60 min. = 10 min. in plasmolytic medium *S* + 9.0 atm. NaCl and 50 min. in *S* + 11.2 atm. NaCl. **d** and **h**: 90 min. = 10 min. in plasmolytic medium *S* + 9.0 atm. NaCl, 50 min. in *S* + 11.2 atm. and 30 min. in *S* + 13.4 atm. NaCl.

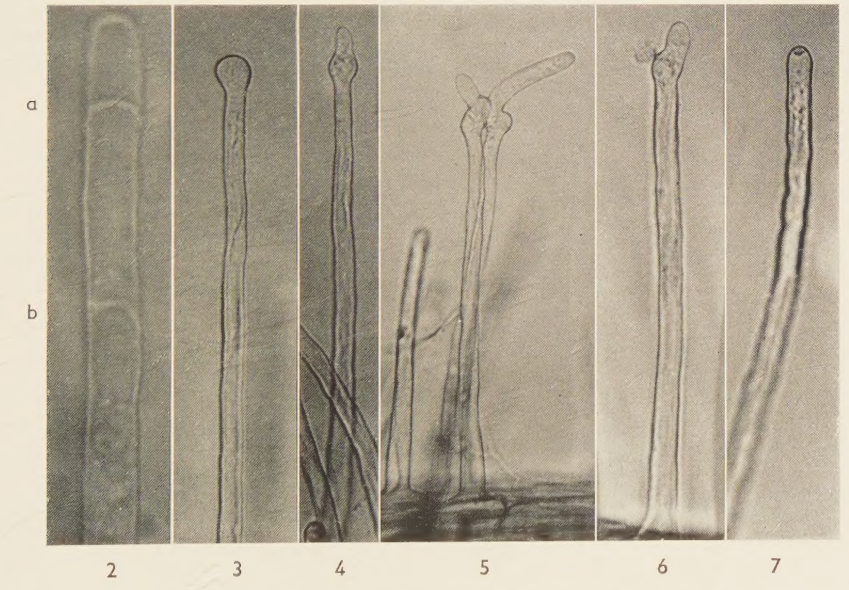

Fig. 2. New cell wall formed inside the original wall by the free apical surface of the contracted protoplast in a plasmolyzed root hair. The new wall (a) was made free by repeated plasmolysis with a more hypertonic solution. Surface of the contracted protoplast at (b). See the text p. 21. Magnification *c.* 600 ×.

Fig. 3. Root hair apex distended after ceased elongation. Observe the thickened apical wall. See the text p. 25. Magnification *c.* 250 ×.

Figs. 4 and **5.** Resumed growth from distended root hair apices. Observe the marked difference between the thickened cell wall of the distended portion and the wall of the new hair portion. See the text pp. 38, 63. Magnification: **fig. 4** *c.* 250 ×, **fig. 5** *c.* 200 ×.

Fig. 6. Resumed growth from a plasmoptyzed root hair. See the text p. 46.

Fig. 7. Root hair with the apical wall stiffened immediately after disturbance. Wall material precipitated at the extreme apical point of the hair. See the text p. 26. Magnification *c.* 250 ×.

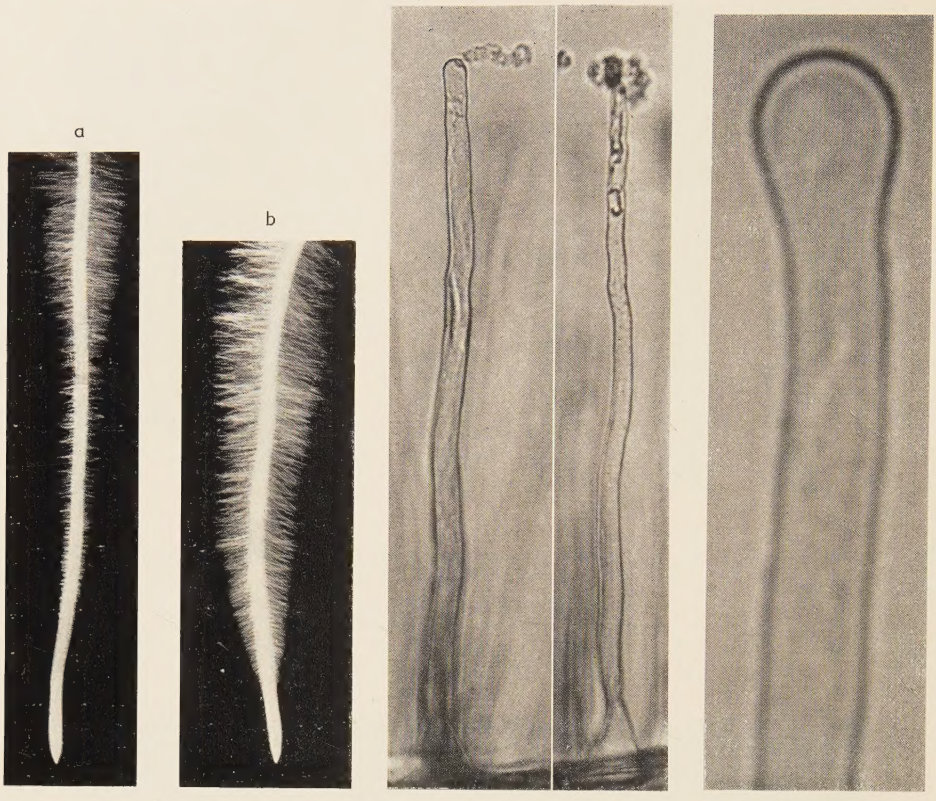

Fig. 8. Development of root hairs in different media. **a.** Root hairs developed in *S*-solution. **b.** Root hairs developed in moist air. See the text p. 56. Magnification *c.* 3 ×.

Fig. 9. Root hair weakly plasmoptyzed after 10 min. treatment with 0.12 *M* NaCl-solution. See the text p. 17. Magnification *c.* 250 ×.

Fig. 10. Root hair highly plasmoptyzed after 70 min. treatment with 0.12 *M* NaCl-solution. Observe the contraction of the hair in the transverse direction compared with **fig. 9.** See the text p. 17. Magnification *c.* 250 ×.

Fig. 11. Root hair apex distended after ceased elongation. Observe the thickened apical wall. See the text p. 25. Magnification *c.* 1 000 ×.

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